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Quantitative Composition and Distribution of the Macrobenthic Invertebrate Fauna of the Continental Shelf Ecosystems of the Northeastern United States

Roger B. Theroux
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CONTENTS

Introduction 1
Order of Discussion 2
Previous Studies 2
Materials and Methods 5
Macrofauna Samples 5
Sampling Gear 6
Sample Processing 6
Data Treatment 8
Geographic Areas 8
Bottom Sediments 9
Bathymetry 10
Temperature 10
Sediment Organic Carbon 11
Description of the Region 11
Topography 11
Bottom Sediments 13
Sediment Organic Carbon 14
Hydrography 14
Zoogeography 16
Faunal Composition 19
Total Macrobenthos—All Taxonomic Groups Combined 28
Geographic Distribution 28
Bathymetric Distribution 40
Relation to Bottom Sediments 47
Relation to Water Temperature 51
Relation to Sediment Organic Carbon 53
Taxonomic Groups 55
Porifera 56
Coelenterata 71
Hydrozoa 71
Anthozoa 75
Alcyonaria 75
Zoantharia 79
Platyhelminthes 81
Turbellaria 81
Nemertea 85
Aschelminthes 91
Nematoda 91
Annelida 94
Pogonophora 100
Sipunculida 103
Echiura 108
Priapulida 108

Mollusca 110
Polyplacophora 110
Gastropoda 119
Bivalvia 124
Scaphopoda 130
Cephalopoda 135
Arthropoda 139
Pycnogonida 139
Arachnida 143
Crustacea 143
Ostracoda 144
Cirripedia 145
Copepoda 155
Cumacea 155
Tanaidacea 159
Isopoda 162
Amphipoda 165
Mysidacea 170
Decapoda 174
Bryozoa 178
Brachiopoda 181
Echinodermata 185
Crinoidea 186
Holothuroidea 187
Echinoidea 192
Ophiuroidea 199
Asteroidea 205
Hemichordata 208
Chordata 210
Ascidiacea 210
Dominant Components of the Macrobenthos 214
Frequency of Occurrence 216
Percentage Composition 216
Geographic Distribution 216
Selected Genera and Species 217
Phylum Annelida 217
Phylum Mollusca 217
Phylum Anthropoda 217
Phylum Echinodermata 224
Bathymetric Distribution 224
Relation to Bottom Sediments 225
Relation to Water Temperature 225
Relation to Sediment Organic Carbon 226
Acknowledgments 227
Literature Cited 227

Quantitative Composition and Distribution of the Macrobenthic Invertebrate Fauna of the Continental Shelf Ecosystems of the Northeastern United States

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ABSTRACT

From the mid-1950's to the mid-1960's a series of quantitative surveys of the macrobenthic invertebrate fauna were conducted in the offshore New England region (Maine to Long Island, NewYork). The surveys were designed to 1) obtain measures of macrobenthic standing crop expressed in terms of density and biomass; 2) determine the taxonomic composition of the fauna (ca. 567 species); 3) map the general features of macrobenthic distribution; and 4) evaluate the fauna's relationships to water depth, bottom type, temperature range, and sediment organic carbon content. A total of 1,076 samples, ranging from 3 to 3,974 m in depth, were obtained and analyzed.

The aggregate macrobenthic fauna consists of 44 major taxonomic groups (phyla, classes, orders). A striking fact is that only five of those groups (belonging to four phyla) account for over 80% of both total biomass and number of individuals of the macrobenthos. The five dominant groups are Bivalvia, Annelida, Amphipoda, Echninoidea, and Holothuroidea.

Other salient features pertaining to the macrobenthos of the region are the following: substantial differences in quantity exist among different geographic subareas within the region, but with a general trend that both density and biomass increase from northeast to southwest; both density and biomass decrease with increasing depth; the composition of the bottom sediments significantly influences both the kind and quantity of macrobenthic invertebrates, the largest quantities of both measures of abundance occurring in the coarser grained sediments and diminishing with decreasing particle size; areas with marked seasonal changes in water temperature support an abundant and diverse fauna, whereas a uniform temperature regime is associated with a sparse, less diverse fauna; and no detectable trends are evident in the quantitative composition of the macrobenthos in relation to sediment organic carbon content.

Introduction

The broad continental shelf off the northeastern coast of the United States is a particularly significant topographic feature of the continental margin because of its influence on the marine life of the region. Water masses overlying this large shelf, and neritic waters generally, are noted for their abundance of plankton, fishes, and associated organisms, some endangered. Noteworthy of the offshore New England waters, including Georges Bank, are the rich harvests of fish that have been taken each year since pre-Colonial days. The marine life inhabiting New England offshore waters has been the subject of studies conducted from time to time throughout the past century. This has resulted in the acquisition of a considerable body of knowledge on the fishes and plankton in this region, but information about the benthic invertebrates has been rather limited, espe-

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cially regarding quantitative aspects. Because of the key role played by macrobenthic invertebrates in the ecological dynamics of the marine environment, their usefulness to man as a food resource, their potential as concentrators of toxic substances that could be transmitted through the food chain, and their usefulness as indicators of environmental change, the National Marine Fisheries Service (formerly the Bureau of Commercial Fisheries) of the U.S. Department of Commerce, NOAA, in cooperation with the U.S. Geological Survey and the Woods Hole Oceanographic Institution conducted a quantitative survey of the benthos of the entire continental margin of the eastern United States. The investigation of the macrobenthic invertebrates was an integral part of a broad program of study of the Atlantic continental margin (Emery and Schlee, 1963; Emery, 1966b).

This report is the second of two which describe the quantitative distribution of macrobenthic invertebrates of the Atlantic continental shelf and slope. The first (Wigley and Theroux, 1981) describes the quantitative distribution of major taxonomic groups of macrobenthic invertebrates inhabiting the continental shelf and slope between Cape Cod, Massachusetts, and Cape Hatteras, North Carolina. Their distribution in relation to geographic location, water depth, bottom sediments, range in bottom water temperature, and sediment organic carbon content is considered.

The present report describes the quantitative distribution of the principal groups of macrobenthic invertebrates inhabiting offshore New England waters. The area studied extends from the mouth of the Bay of Fundy eastward to Nova Scotia (longitude 64° West) and southward to central New Jersey. The quantity of each major taxonomic group is considered in relation to the same environmental variables. Only the broad distributional aspects of major groups are presented and evaluated here. Other aspects of the benthic fauna derived from these samples, such as community composition, trophic zonation, faunal dominance and diversity, and similar topics will be the subjects of future reports.

The large database generated by the Continental Margin Program contains a wealth of valuable geological, faunal, and environmental information of historical as well as current significance. In addition to providing input for a variety of descriptive studies, as described above, the potential exists for information contained in the database for ecosystem modeling tasks; paleoecological and global climate change studies; and benthic production estimates (Cohen et al. 1978, 1982; Cohen and Wright 1979; Warwick 1980; Rowe et al. 1986, 1988; Bourne 1987; Cohen and Grosslein 1987; Steimle 1987, 1990a, 1990b; Rowe et al., 1991; and others).

Order of Discussion

The first section of this report briefly describes the principal physical features of the region, providing a general background for understanding the distribution of the various faunal groups. This section is followed by the main body of data describing the quantitative distribution of 44 faunal groups in relation to the five environmental parameters: 1) geography, 2) bathymetry, 3) bottom sediments, 4) bottom water temperatures, and 5) sediment organic carbon. Quantitative data for geographic distribution are presented at two different levels: a detailed evaluation based on calculations for each of several hundred unit areas (20 min in latitude by 20 min in longitude); and a less detailed evaluation based on six large geographical subareas within the region studied. Faunal groups are chiefly phyla, classes, and orders of macrobenthos presented in phylogenetic order. The final section is a summary of the environmental relationship of the dominant taxonomic components.

Previous Studies

One of the earliest studies in marine benthic ecology dealt with populations inhabiting the Woods Hole-Vineyard Sound area off southeastern Massachusetts (Verrill et al., 1873). This well-known study is not only the first comprehensive report dealing with the New England marine benthos but also one of the earliest ecological accounts of marine zoobenthos in all scientific literature. Included in the report are descriptions of new species, an annotated catalog of animals found in Vineyard Sound and vicinity, and, significantly, a large part of the report is devoted to descriptions of the benthic communities and the biotopes they inhabit. Although a small number of published reports on New England natural history observations and taxonomic studies were available as sources of information to supplement their study (Gould 1841, 1870; Desor 1851; Stimpson 1851, 1853; Verrill 1867; and others), by far the bulk of all information contained in the report by Verrill et al. is based on original collections and observations.

Between 1871 and 1887 nearly 2,000 benthic fauna samples were collected in waters off the northeastern United States by the U.S. Fish Commission in cooperation with the U.S. Revenue Service, U.S. Coast Survey, and zoologists from American universities. Dredging and trawling were the principal methods of collecting samples. A large proportion of the samples were collected in coastal areas between New Haven, Connecticut, and Eastport, Maine; only a moderate number of collections were from offshore areas. Inshore operations were conducted from the vessels *Moccasin, Mosswood, Bache, Speedwell, Blue Light,* and to some ex-

tent the *Blake* and *Fish Hawk*; however, the latter two also operated in offshore areas, as did the *Albatross* and the chartered fishing schooner, *Josie Reeves* (Packard, 1874, 1876: Agassiz, 1881; Smith and Rathbun, 1882; Tanner, 1882; Smith and Rathbun, 1889; Townsend, 1901).

This early sampling was primarily exploratory in nature. The participating zoologists faced a vast unstudied fauna and a multitude of species new to science. Scientists most active in this work were chiefly systematists; consequently the results were largely taxonomic accounts of various groups. The following are typical examples: Smith, 1879, 1884; Harger,1880, 1883; Rathbun, 1880; Wilson, 1880; Fewkes, 1881; Verrill ,1881, 1884; Agassiz, 1883, Webster and Benedict, 1884; Bush, 1885; Bigelow, 1891). Professor Addison E. Verrill of Yale College, who collaborated closely with U.S. Fish Commission scientists, was undoubtedly the most productive systematist of this, or perhaps any era. He described over one thousand species representing most major invertebrate groups. A very large percentage of these new species descriptions was based on specimens collected off New England. Although several preliminary ecological studies of the offshore benthos were reported (Smith and Harger, 1874; Verrill, 1874a, 1874b; Agassiz 1888a, 1888b) and the reports on systematics of various groups contain ecological information, no comprehensive ecological reports pertaining to the fauna of this region were published.

The second milestone in ecological research of the New England marine benthos was a comprehensive report by Summer et al. (1913). This report is based on three years of intensive sampling in Vineyard Sound and Buzzards Bay by the Bureau of Fisheries in 1903, 1904, and 1905. This useful publication not only lists the species occurring in the Woods Hole region but includes species distribution charts and discusses some physical conditions (temperature, depth, and sediments) that influence the distribution of animals. To this day, this remains the most thorough ecological study of the New England marine benthos.

After the investigation by Sumner et al. (1913), there was a 30-year hiatus during which ecological research on New England marine benthos—particularly that concerned with offshore invertebrates—proceeded at an exceedingly slow pace. Belding (1914), Allee (1922a, 1922b, 1923a, 1923b, 1923c), Pytherch (1929), Stauffer (1937), Ayers (1938), and others contributed valuable information on inshore populations. Rather few ecologically oriented works such as Procter (1933a, 1933b) and Bigelow and Schroeder (1939) pertaining to offshore zoobenthos appeared during this period. In addition to the foregoing, however, many studies of a taxonomic nature containing valuable ecological information were issued during this time span (Rathbun, 1905, 1925; Koehler, 1914; Nutting, 1915; Pilsbry, 1916; Heath, 1918; Bartsch, 1922; Deichmann, 1930, 1936; and others). Ecological interests of marine scientists conducting field studies in this region centered on plankton and fishes. It was not until the 1940's that renewed activities in benthic ecology attained a significant level. Beginning in that decade a number of investigations were undertaken concerning inshore populations (Dexter, 1944, 1947; Lee, 1944; Phleger and Walton, 1950; Swan 1952a, 1952b; Parker, 1952; Pratt, 1953; Burbanck et al., 1956; Parker and Athern, 1959; Stickney, 1959; Rhoads, 1963; and others). Ecological studies pertaining to the offshore populations commenced somewhat later, for example the reports by: Parker (1948); Northrup (1951); Phleger (1952); Clarke (1954); Schroeder (1955, 1958); Taylor et al. (1957); Wigley (1959); Wieser (1960); Wigley (1960b); Chamberlin and Stearns (1963); and Wigley and Emery (1968), are notable examples.

Perhaps the most significant event of this period, relative to the present work, was the inauguration of quantitative benthos investigations of the New England marine fauna (Lee, 1944). Lee's work was a study of the macrobenthic invertebrate fauna of Menemsha Bight, an embayment of Vineyard Sound, Massachusetts. Years later, quantitative studies were made of the benthos of Long Island Sound (Sanders, 1956; Richards and Riley, 1967), Buzzards Bay (Sanders, 1958, 1960; Wieser, 1960), Barnstable Harbor (Sanders et. al., 1962), Greenwich Bay, Rhode Island (Stickney and Stringer, 1957), Sheepscot Estuary (Hanks, 1964), Narragansett Bay (Phelps, 1965), Rand's Harbor, Massachusetts (Burbanck et al., 1956), and other locales. In recent years, due to increased interest in potential impacts of man's activities in outer continental shelf (OCS) development and exploitation and in understanding the dynamics of marine ecosystems, quantitative studies of the benthic fauna in the New England region have undergone a marked increase, as have studies in other associated disciplines. Studies such as Wigley (1961b); Sanders et. al. (1962); Wigley and McIntyre (1964); Emery et al. (1965); Nesis (1965); Sanders et al. (1965); Owen et al. (1967); Wigley and Emery (1967); Wigley (1968); Mills (1969); Wigley and Theroux (1970); Haedrich, et al. (1975); Rowe et al. (1975); Wigley et al. (1975); Uzmann et al. (1977); Pearson and Rosenberg (1978); Maurer and Leathem (1980, 1981a, 1981b); Valentine et al. (1980); Magnuson et. al. (1981); Wigley and Theroux (1981); Maurer and Wigley (1982, 1984); Steimle (1982); Caracciolo and Steimle (1983); Lear and O'Malley (1983); Steimle (1985); Rowe et al. (1986); Maciolek and Grassle (1987); Michael (1987); Theroux and Grosslein (1987); Langton et al. (1988); Langton and Uzmann (1988); Sherman et al. (1988); Langton and Uzmann 1989, Langton et. al. (1990); and Rowe et. al. (1991), and as well as others have provided much needed insights into the complex ecosystems of the region.

Several published indexes and bibliographies include many references to the general literature pertaining to benthic invertebrates and allied subjects. Many of the historical as well as the modern reports are included among the citations in these bibliographies.

The interested reader may wish to consult the following:

1 Fishery Publication Index, 1920–1954. U.S. Fish & Wildlife Service Circular 36, published in 1955.
2 Publications of the United States Bureau of Fisheries 1871–1940. Compiled by Barbara B. Aller and published in 1958.
3 A Preliminary Bibliography with KWIC Index on the Ecology of Estuaries and Coastal Areas of the Eastern United States. Compiled by Robert Livingston Jr. and published in 1965.
4 Marine and Estuarine Environments, Organisms and Geology of the Cape Cod Region, an Indexed Bibliography, 1665–1965. Compiled by Anne E. Yentsch, M. R. Carriker, R. H. Parker, and V .A. Zullo, published in 1966.
5 Fishery Publication Index, 1955–64. U.S. Fish & Wildlife Service, Bur. Comm. Fish. Circ. 296, published in 1969.
6 The Effects of Waste Disposal in the New York Bight. Compiled by the National Marine Fisheries Service, Middle Atlantic Coastal Fisheries Center, Sandy Hook, New Jersey, published in 1972.
7 Coastal and Offshore Environmental Inventory: Cape Hatteras to Nantucket Shoals. Edited by Saul B. Saila and published in 1973.
8 Bibliography of the New York Bight: Part 1—List of Citations; Part 2— Indices. Compiled by the National Oceanic and Atmospheric Administration, Marine Ecosystems Analysis Program, Stony Brook, N.Y, published in 1974.
9 Fishery Publication Index, 1965–74. Compiled by M. E. Engett and L. C. Thorson, U.S. Dep. Commerce, NOAA Tech. Rep. NMFS Circ. 400, published in 1977.
10 A Summary and Analysis of Environmental Information on the Continental Shelf from the Bay of Fundy to Cape Hatteras (1977). Vol. II, Master Bibliography, Index, Acknowledgements. Prepared for the Bureau of Land Management by Center for Natural Areas, published in 1977.
11 The Bay Bib: Rhode Island Marine Bibliography, Revised Edition. Coordinated by C. Q. Dunn and L. Z. Hale, edited by A. Bucci, Coastal Resources Center, Northeast Regional Coastal Information Center, Marine Advisory Service, National Sea Grant Depository, Univ. of Rhode Island Mar. Tech. Rep. 70, published in 1979.
12 An Ecological Characterization of Coastal Maine (North and East of Cape Elizabeth). Vol. 5, Data Source Appendix. Compiled by S. E. Fefer and P. A. Schetting for Biol. Serv. Program, Interagency Energy/Environment Res. and Dev. Program, Office of Res. and Dev., U.S. Environmental Protection Agency, published in 1980.
13 Benthic Productivity and Marine Resources of the Gulf of Maine. I. Babb and M. DeLuca (eds.). National Undersea Research Program, Research Report 88-3, published in 1988.

Another result of increased OCS activity is the large volume of information relating to benthic fauna appearing in the so-called "gray" literature. Included in this category are completion reports of field study contracts, environmental impact statements, public and private agency investigation reports, annual reports, and other similar special documents. Many appear in irregular series, or are one-of-a-kind reports, often in photocopied or mimeographed form and, as such, are not always listed in the usual literature sources (e.g. Maurer, 1983; Michael et. al., 1983; Pratt, 1973; also see Literature Cited).

In addition to Wigley and Theroux (1981) there are several taxonomically or ecologically oriented reports based wholly or in part on the samples forming the basis of the Northeast Fisheries Science Center (NEFC) benthic database. Such reports include Wigley (1960a, 1960b, 1961a, 1961b, 1963a, 1963b, 1965, 1966a, 1966b, 1968, 1970, and 1973); Pettibone (1961, 1962, 1963); Chamberlin and Stearns (1963); Emery and Merrill (1964); Wigley and McIntyre (1964); Emery et al. (1965); Trumbull (1965); Merrill et al. (1965); Wigley and Shave (1966); Wigley and Emery (1967); Schopf (1968b); Haynes and Wigley (1969); Plough (1969); Hazel (1970); Merrill (1970); Wigley and Theroux (1970); Kraeuter (1971); Wigley and Burns (1971); Wigley and Theroux (1971); Bousfield (1973); Cutler (1973, 1977); Wigley and Stinton (1973); Murray (1974); Wigley et al. (1975); Wigley and Messersmith (1976); Wigley et al. (1976); Williams and Wigley (1977); Kinner (1978); Merrill et al. (1978); Plough (1978); Brodeur (1979); Watling (1979a); Dickinson et al. (1980); Franz and Merrill (1980b); Dickinson and Wigley (1981); Franz et al. (1981); Maurer and Wigley (1982, 1984); Maurer (1983); Shepard and Theroux (1983); Theroux[1]; Theroux and Wigley (1983); Rowe et al. (1986); Shepard et al. (1986); Bousfield (1987); Rowe (1987); Theroux and Grosslein (1987); Langton and Uzmann (1988); Langton et al. (1988); Rowe et al. (1988); Sherman et al. (1988); Langton and Uzmann (1989); Langton et al. (1990);

[1] Theroux, R. B. 1983. Collection data for the U.S. east coast gastropod mollusks in the Northeast Fisheries Center Specimen Reference Collection, Woods Hole, Massachusetts. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Cntr., Woods Hole Lab. Ref. Doc. No. 8327, 280 p. Unpubl. manuscript.

and Rowe et al. (1991); Burns and Wigley[2]; Wigley et al.[3]; Theroux and Wigley[4]; Maurer and Wigley[5]; Theroux, et al.[6]; Theroux and Schmidt-Gengenback.[7]

Other uses to which the data have proven useful in the past, as well as in the present, have been varied. Included have been environmental impact statements prepared by various public agencies (Dep. Interior, Minerals Management Service; U.S. Army Corps of Engineers; NOAA, etc.) relating to OCS activities (e.g. oil and gas exploration, mining, dredging, dumping, etc.); international litigation (i.e. US/Canada Boundary Case); marine sanctuary designation proposals (e.g. Stellwagen Bank, Norfolk Canyon); and others.

Several specially targeted programs initiated in the latter 1970's and terminated in the mid- to late 1980's have provided additional impetus for an increase in attention devoted to the macrobenthos of the region. During that period many studies were conducted by public and private agencies and academic institutions (e.g. NOAA's Northeast Monitoring and Ocean Pulse Programs; the Northeast Fisheries Center's Marine Resources Mapping, Assessment, and Prediction program (Sherman, 1980); the Marine Ecosystem Analysis Program (MESA) (see Pearce et al., 1981); the Woods Hole Oceanographic Institution's Georges Bank Study program, and many others). Those studies, in both inshore and offshore areas, were designed to establish baselines for assessing environmental quality and to monitor the impacts of present and future activities related to oil and gas exploration and production, marine mining, ocean dumping, other waste disposal, and natural environmental change. The results of those programs covered a broad spectrum of interdisciplinary topics which expanded our understanding of the marine environment (e.g. Pearce, 1971, 1972, 1974, 1975; Pratt, 1973; Pearce et al., 1976a, 1976b, 1976c, 1976d, 1977a, 1977b, 1977c, 1978, 1981; Caracciolo et al., 1978; Pearson and Rosenberg, 1978; Reid et al., 1979; Steimle and Radosh, 1979; Warwick, 1980; Schaffner and Boesch, 1982; Steimle, 1982; Boehm, 1983; Caracciolo and Steimle, 1983; Lear and O'Malley, 1983; Steimle, 1985; Steimle and Terranova, 1985; Duinker and Beanlands, 1986; Howart,1987; Neff, 1987; Reid et al., 1987; Steimle, 1990a, 1990b; Steimle et al., 1990).

Materials and Methods

Macrofauna Samples

This report is based on 1,076 quantitative samples of macrobenthic fauna collected during 22 cruises by 5 research vessels between 1956 and 1965 (Table 1). The geographic locality of sampling sites is illustrated in Figure 1, and sampling density is illustrated in Figure 2 in which the number of samples in each geographic unit area is indicated (dimension of each unit area is 20 minutes latitude by 20 minutes longitude). Collection data (including cruise, station, and collection num-

Table 1
Research vessels, cruise numbers, date of collections, and number of samples obtained.

Vessel	Cruise number	Date	Number of samples
Albatross III	80	August 1956	35
Albatross III	101	August 1957	165
Delaware	59-9	August 1959	75
Delaware	61-10	June 1961	75
Delaware	62-7	June 1962	123
Gosnold	10	April 1963	7
Gosnold	11	April 1963	3
Gosnold	12	May 1963	38
Gosnold	13	May 1963	29
Gosnold	20	July 1963	1
Gosnold	22	August 1963	93
Gosnold	24	August–September 1963	32
Gosnold	28	October 1963	9
Gosnold	29	October 1963	84
Gosnold	49	August 1964	72
Gosnold	51	September 1964	7
Asterias	1	April 1964	8
Asterias	2	July–August 1964	62
Albatross IV	64-12	October 1964	24
Albatross IV	64-13	October–November 1964	10
Albatross IV	65-11	August 1965	123
Total			1,076

[2] Burns, B. R., and R. L. Wigley. 1970. Collection and biological data pertaining to mysids in the collection at the BCF Biological Laboratory, Woods Hole. U.S. Bur. Comm. Fish. Biol. Lab. Woods Hole, Mass., Lab. Ref. 70-3, 36 p. (mimeo). Unpubl. manuscript.

[3] Wigley, R. L., R. B. Theroux, and H. E. Murray. 1976. Marine macrobenthic invertebrate fauna of the Middle Atlantic Bight region. Part 1. Collection data and environmental measurements. Northeast Fisheres Center, Woods Hole Lab. Ref. Doc. 7618, 34 p. (mimeo). Unpubl. Manuscript.

[4] Theroux, R. B., and R. L. Wigley. 1979. Collection data for U.S. east coast bivalve mollusks in the Northeast Fisheries Center Specimen Reference Collection, Woods Hole, Massachusetts. Northeast Fisheries Center, Woods Hole Laboratory, National Marine Fisheries Serv., NOAA, Northeast Fisheries Center.,Woods Hole Lab. Ref. Doc. 79-29, 471 p. (mimeo). Unpubl. Manuscript.

[5] Maurer, D., and R. L. Wigley. 1981. Distribution of biomass and density of macrobenthic invertebrates on the continental shelf off Martha's Vineyard, Massachusetts. National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole Laboratory, NOAA, Woods Hole Lab. Ref. Doc. 81-15, 97 p. (mimeo). Unpubl. manuscript.

[6] Theroux, R. B., R. L. Wigley, and H. E. Murray. 1982. Marine macrobenthic invertebrate fauna of the New England Region: Collection data and environmental measurements. Nat. Mar. Fish. Serv., NOAA, Northeast Fish. Center, Woods Hole Lab. Ref.Doc. 82-40, MARMAP Contrib. MD/NEFC 82-67, 74 p. (mimeo). Unpubl. Manuscript.

[7] Theroux, R. B., and J. Schmidt-Gengenbach. 1984. Collection data and environmental measurements for U.S. east coast Cumacea (Arthropoda, Crustacea) in the Northeast Fisheries Center Specimen Reference Collection Woods Hole, Massachusetts. Nat. Mar. Fish. Serv., Northeast Fisheries Center, Woods Hole Lab. Ref. Doc. 84-27, MARMAP Contr. MED/NEFC 83-46, 114 p. (mimeo). Unpubl. Manuscript.

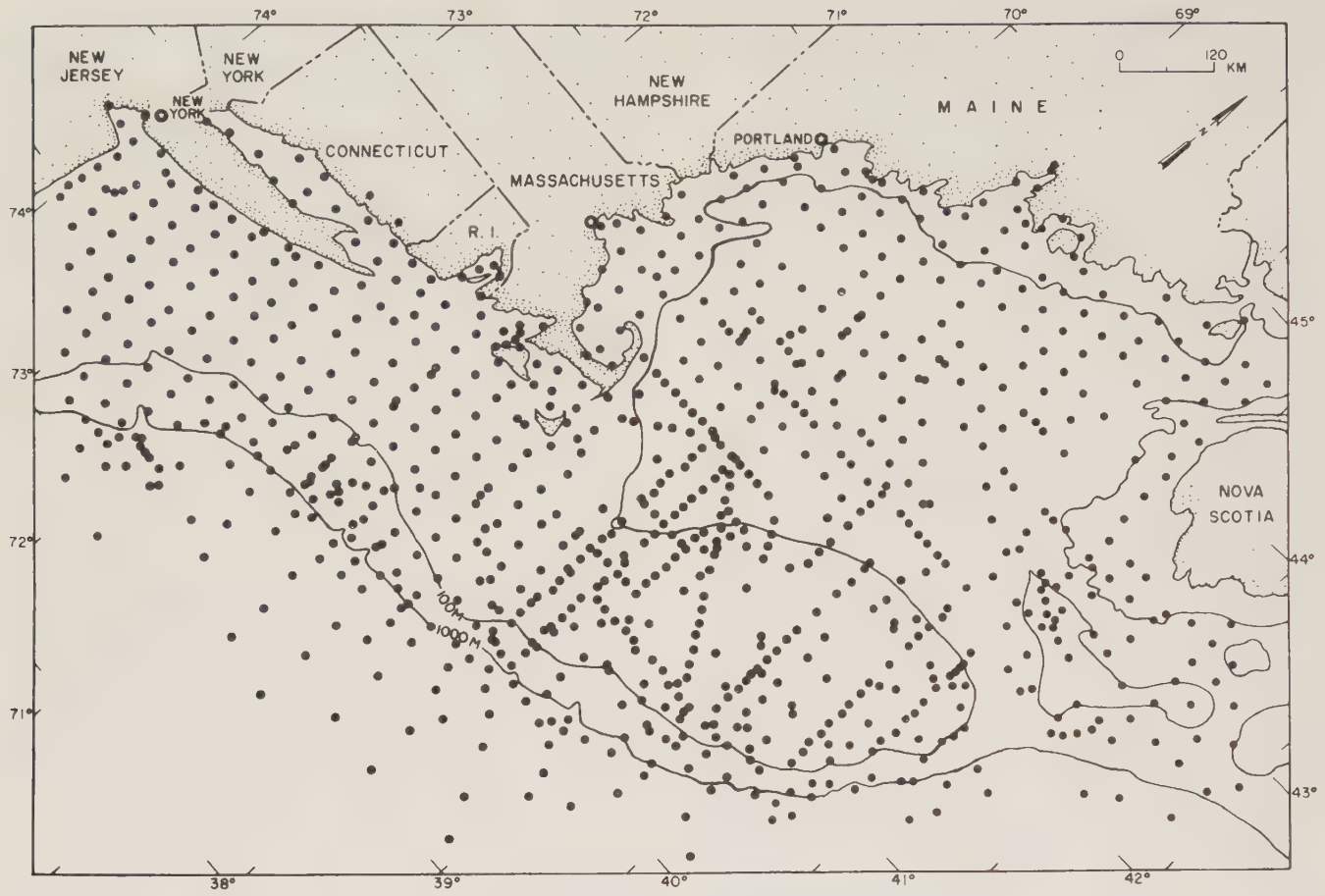

Figure 1

Chart of the study area showing the location of stations where quantitative samples of macrobenthic invertebrates were obtained.

bers, number of samples, latitude, longitude, date of sampling, and type of gear used) and environmental measurements (including water depth in meters, bottom type, geographic subarea, temperature range [°C], and percent organic carbon) for each sampling site are contained in Theroux et al.[6]).

Sampling stations were located in all sections of the study area, but somewhat more intensive coverage was given to the offshore continental shelf region than to the inshore bays and sounds or to the deep water region beyond the continental shelf. Table 2 lists the number of samples and occurrence frequency for each parameter grouping. A moderate number of samples, however, were taken in the major bays and estuaries, and in deep water. Ninety-two samples were collected at depths less than 24 m, and 93 samples from depths greater than 500 m. The continental rise was only sparsely sampled because of its great depth and the correspondingly increased time required to obtain samples. Minimum and maximum depths at which samples were taken were 3 and 3,975 m.

Sampling Gear

The samples consisted of bottom sediments with the constituent fauna collected with a Smith-McIntyre spring-loaded grab sampler (Smith and McIntyre, 1954) illustrated in Figure 3, or a Campbell grab sampler (Menzies et al., 1963) illustrated in Figure 4. The bottom area sampled by the Smith-McIntyre sampler was 0.1 m^2 which had a capacity of approximately 15 liters (L). Area sampled by the Campbell sampler was 0.56 m^2, which had a volume capacity of about 200 L. The Campbell grab was equipped with a 35-mm camera and electronic flash, housed within the buckets, to obtain photographs of the bottom immediately before impact (Emery and Merrill, 1964; Emery et al., 1965; Wigley and Emery, 1967; Theroux, 1984).

Sample Processing

Aboard ship, the material obtained at each sampling site by each sampler was processed and preserved as a

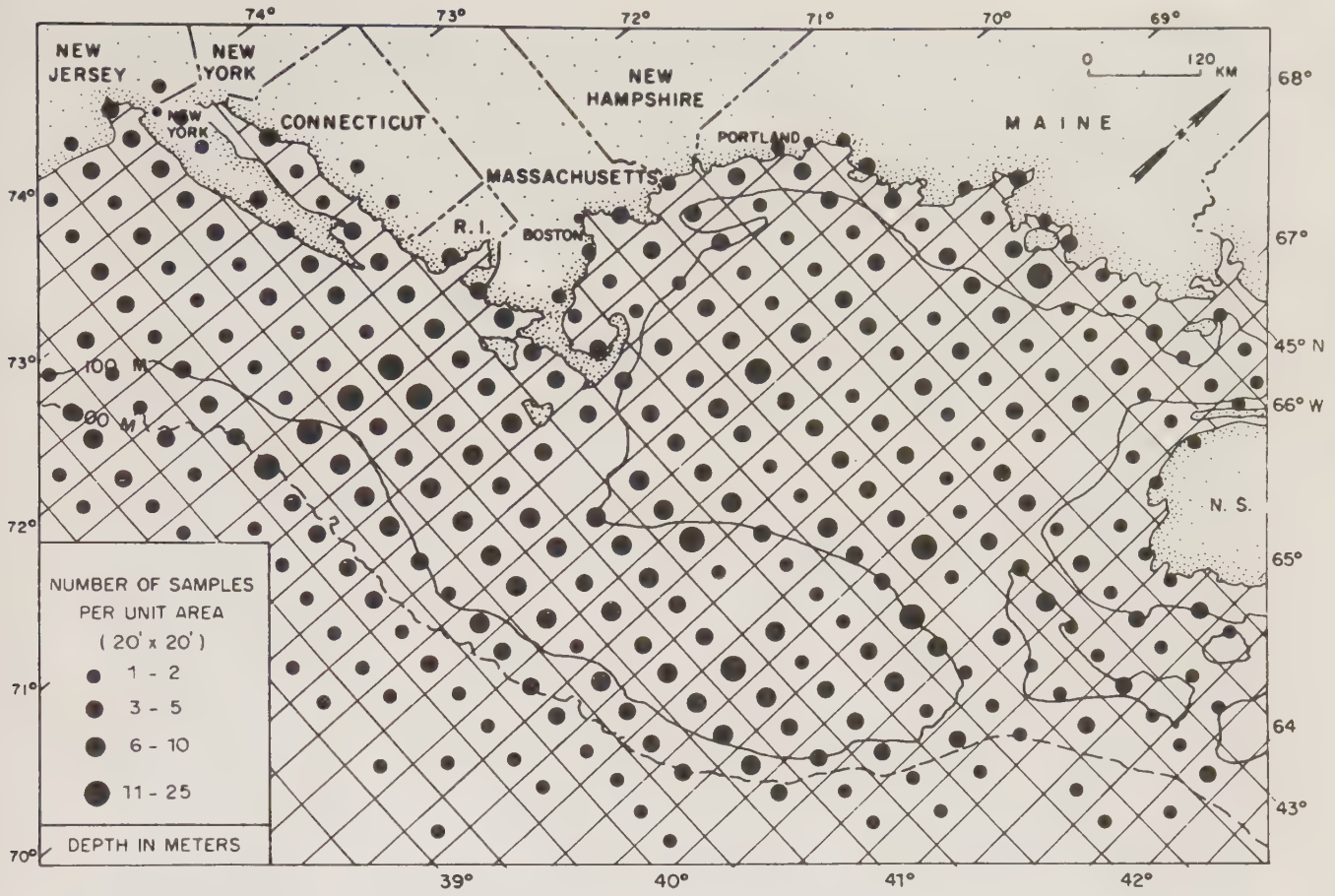

Figure 2

Chart showing sampling intensity within each standard unit area (20 min. latitude by 20 min. longitude). All samples within each unit area have been added to indicate sampling density.

separate sample. The contents of the sampler were emptied into a bucket or tub calibrated in liters, or directly into a wash-box (volume measured by means of a calibrated rule) from which two small subsamples were removed prior to washing. One of these subsamples was for meiofauna, and the other for sediment analysis. Total quantity removed ranged from 0.25 to 1.0 L, depending upon the total volume of material obtained. The quantities of both samples and subsamples were measured and recorded on sample log sheets. Generally, the remaining material was washed through a 1-mm-aperture mesh-sieving screen. Material remaining on the screen after washing, consisting of benthic animals, tubes, shells, shell hash, and coarse sediments, was preserved in a buffered seawater solution of formaldehyde and brought to the laboratory ashore for further processing.

Laboratory processing involved separating the preserved organisms from the mineral debris, sorting them to major taxonomic groups, identifying them to the lowest practicable taxonomic level, counting, and weighing. Weights are damp formalin weight, the "rough weight" of Petersen (1918), herein referred to as wet weight inasmuch as the superficial fluid on the specimens was removed by blotting before being weighed on a Mettler precision balance to the nearest 0.01 g. Weights include shells and skeletal materials that constitute an integral part of the living animal, i.e. shells of living mollusks, brachiopods, and skeletal structures of bryozoans, barnacles, and similar organisms. Materials omitted in the weighing procedure were: tubes of polychaetous worms, gastropod and scaphopod shells inhabited by pagurid crabs or sipunculid worms, and other similar nonintegral structures or nonliving animal remains. Counts of the number of specimens were made for all groups. Colonial animals were treated as individuals; that is, one sponge colony, or a colony of bryozoans was each counted as an individual specimen; colonies are much more comparable in size to individuals of noncolonial animals than are the zooids making up the colony. Also, the disparity in size from smallest to largest colonial organisms was only slightly greater than the size differential between small and large individuals of noncolonial species.

Specimens of each taxon were bottled separately in 70% ethanol and labeled. Subsequently, specimens were assembled by taxonomic groups and sent to cooperating systematists for species determinations. There were more than 40 specialists from the United States and from other countries cooperating in this part of the study.

Data Treatment

Information pertaining to the location, collecting methods, physical and chemical characteristics of the environment, and the number and weight of the biological components of each sample was recorded on preprinted data forms. The coded information and quantitative data from the records were entered on automatic data-processing cards. Data were summarized by computer in a form similar to that presented in the tables appearing in the body of this report.

The principal units used for expressing the quantity of benthic invertebrates (quantity per unit area) are: 1) density—number of individual specimens per square meter of bottom area, and 2) biomass—wet weight, in grams, per square meter of bottom.

Faunal density values used in constructing quantitative geographic distribution charts for the various taxonomic groups (Figs. 12, 27, 33, 39, 45, etc.) are mean values for all samples within each unit area as shown in Figure 2.

Qualitative and quantitative differences between seasons and between years were sufficiently small to permit the consolidation of all samples for purposes of this report. Some seasonal and yearly differences in taxonomic composition and quantity of animals were detected within specific geographic localities that were repeatedly sampled. With few exceptions, however, the dissimilarities were relatively minor in comparison to the differences from one geographic locality to another. One of the chief reasons for the temporal stability was the presence of many animals having a long (one year to a century or more) life span. The common occurrence of sessile forms and nonmigratory motile forms also contributed to the observed constancy in biomass. Similar conditions were reported by Zatsepin (1968, in Steele, 1973) in reference to macrobenthos samples taken in the Barents Sea and Norwegian Sea over a 30-year period. He found that a comparison of samples taken in the same regions in different years ". . . showed no substantial changes in the quantitative distribution of the bottom fauna." Several recent reports also allude to the temporal persistence of certain dominant components of the macrobenthos of the region (Steimle, 1990a, 1990b; Maurer[8]; Michael et al.[9]).

Table 2
Numbers of samples and occurrence frequency in each of the various parameter groupings used in this report.

Parameter	Number of samples	Frequency (%) of occurrence
Geographic area		
Nova Scotia	85	7.9
Gulf of Maine	303	28.2
Georges Bank	211	19.6
Southern New England Shelf	344	32.0
Georges Slope	52	4.8
Southern New England Slope	81	7.5
Depth range (m)		
0–24	92	8.6
25–49	160	14.9
50–99	319	29.6
100–199	246	22.9
200–499	166	15.4
500–999	22	2.0
1000–1999	34	3.2
2000–3999	37	3.4
Sediment type		
Gravel	148	13.8
Till	22	2.0
Shell	6	0.6
Sand	455	42.2
Sand-silt	211	19.6
Silt-clay	234	21.8
Temperature range (°C)		
0–3.9	335	31.1
4–7.9	158	14.7
8–11.9	336	31.2
12–15.9	157	14.6
16–19.9	62	5.8
20–23.9	28	2.6
Sediment organic carbon (%)		
0.00	5	0.5
0.01-0.49	418	38.8
0.50-0.99	167	15.5
1.00-1.49	84	7.8
1.50-1.99	43	4.0
2.00-2.99	13	1.2
3.00-4.99	4	0.4
5.00+	1	0.1
missing data	341	31.7

Geographic Areas

For purposes of detecting and reporting regional differences in faunal composition the region has been

[8] Maurer, D. 1983. Review of benthic invertebrates of Georges Bank in relation to gas and oil exploration with emphasis on management implications. Natl. Mar. Fish, Serv., Northeast Fisheries Center, Woods Hole, Massachusetts, Woods Hole Lab. Ref. Doc. 83-16, 329 p. (mimeo). Unpubl. manuscript.

[9] Michael, A. D., C. D. Long, D. Maurer, and R. A. McGrath. 1983. Georges Bank benthic infauna historical study. Final report to U.S. Dep. Interior, Minerals Management Service, Washington, DC, Rep. 83-1 by Taxon Inc. Salem, MA 01970, 171 p.

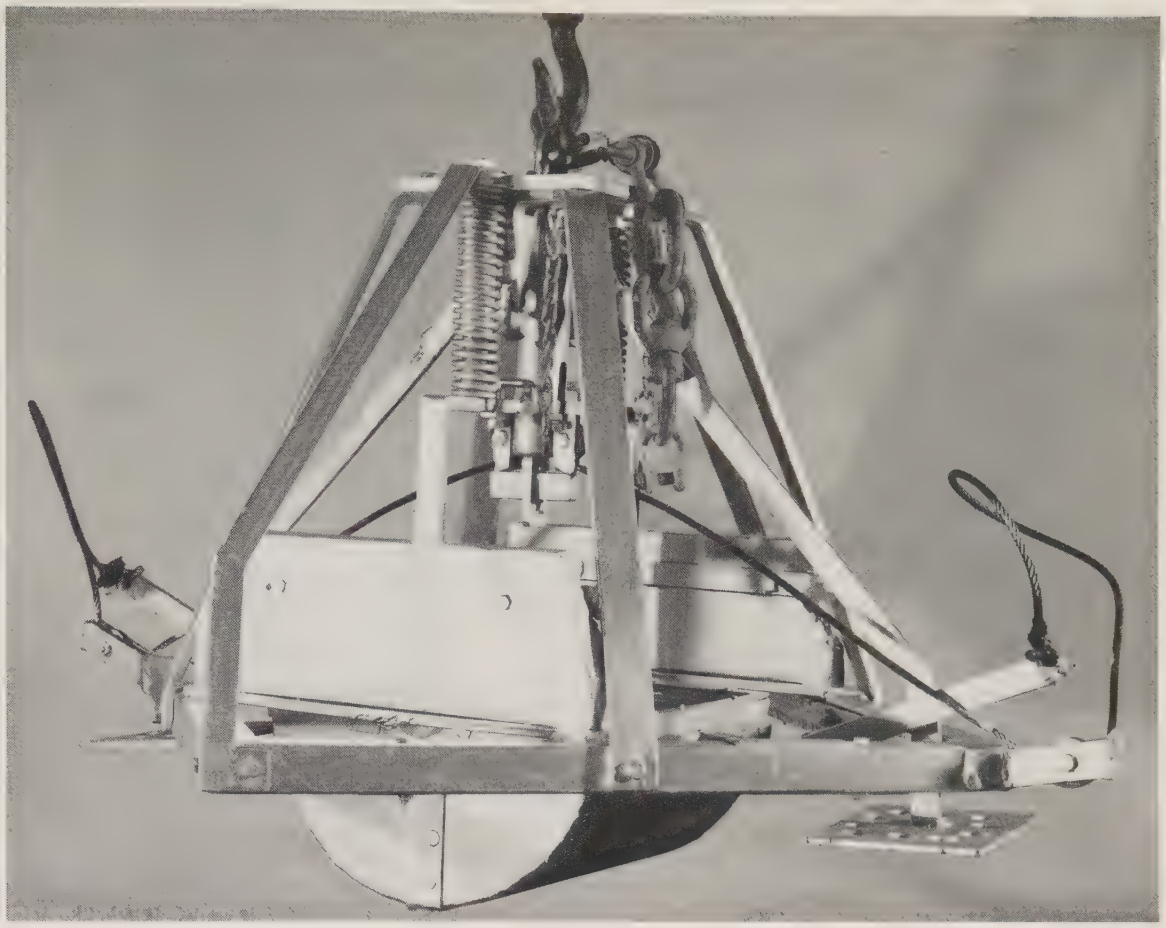

Figure 3
Side view of the Smith-McIntyre spring-loaded bottom sampler in the closed position. Lead weights on each side are set vertically to impede rotation of the sampler during descent and ascent. Vertical distance from frame base to top plate is 52 cm.

divided geographically into six subareas (Fig. 5). These are: 1) Nova Scotia, containing 44,816 km^2 (13,049 mi^2)—encompassing southwestern Bay of Fundy, eastern gulf of Maine, Browns Bank, and the Nova Scotian continental shelf; 2) Gulf of Maine—all of the Gulf of Maine except the eastern sector encompassing an area of 80,067 km^2 (23,313 mi^2); 3) Georges Bank—consisting only of Georges Bank proper with an area of 39,211 km^2 (11,417 mi^2); 4) Southern New England Shelf occupying 73,318 km^2 (21,348 mi^2)—including the continental shelf from Great South Channel southwestward to central New Jersey; 5) Georges Slope—the continental slope from Great South Channel northeasterly to off the Scotian Banks, an area of 50,706 km^2 (14,764 mi^2); 6) Southern New England Slope—the continental slope from Great South Channel southwesterly to southwest of Hudson Canyon, occupying 62,570 km^2 (18,218 mi^2). Each subarea has specific biotopic and biogeographic faunal characteristics. These are discussed in the section entitled "Description of the Region" and in the "Geographic Distribution" section for each of the major taxonomic groups.

Bottom Sediments

Bottom sediments from the samples have been analyzed for particle size, composition, and color. In addition, a selected series of these samples was further analyzed for carbonate content (Hülsemann, 1966), quantity of organic matter (Hülsemann, 1967) and minerology (Ross, 1970b). Detailed particle size analyses of approximately 75% of the samples were made by John Schlee, U.S. Geological Survey (Schlee, 1973).

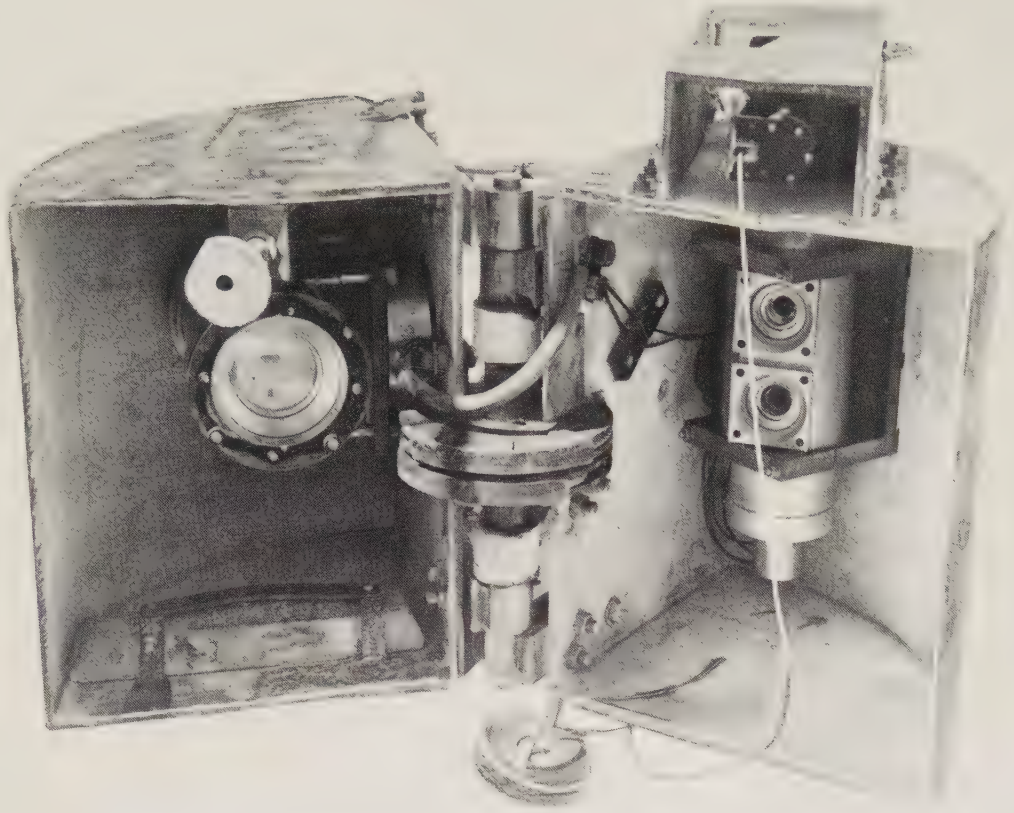

Figure 4
Bottom view of Campbell grab sampler. Camera housing is installed in right-hand bucket and strobe light is in the left-hand bucket. Shutter trip weight is in foreground. Width of the buckets (vertical dimension in photograph) is 57 cm.

Approximately 20% of the samples were analyzed by the New York Soil Testing Laboratory (Wigley, 1961a). The remaining 5% were classified using field techniques by K.O. Emery of the Woods Hole Oceanographic Institution or by National Marine Fisheries Service personnel. For additional information concerning sediment analyses, methodology, and detailed results, see references listed by Emery (1966b) and the section of this report titled "Description of the Region."

Bathymetry

Water depths, in meters, were obtained by means of echo sounders and precision depth recorders and corrected for hydrophone/transducer depth and temperature effects on the velocity of sound in water.

Temperature

Water temperature and salinity data were based primarily on the hydrographic report prepared by John B. Colton et al. (1968), which gives detailed information obtained on eight quarterly (March, May, September, and December) hydrographic survey cruises from 1964 to 1966. Each cruise covered the entire area from Nova Scotia to New York. We also used several thousand bottom temperature records obtained on seventeen bottom trawl survey cruises of the research vessels *Albatross III, Albatross IV,* and *Delaware,* conducted by the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, during the years 1956 through 1965. Additional sources of reference and temperature-salinity data are: Townsend (1901); Sumner, et al. (1913); Bigelow (1927, 1933); Edwards et al. (1962); Hathaway

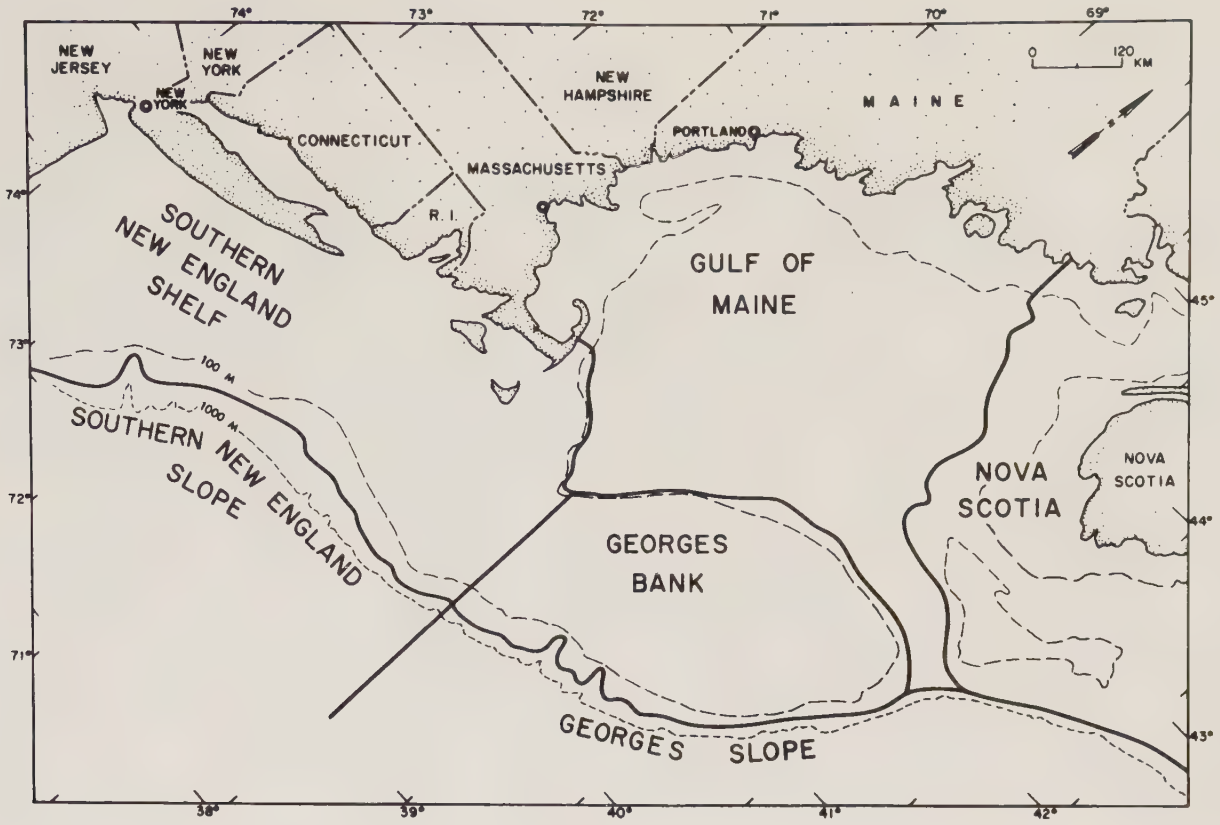

Figure 5

Chart of the study area showing the location of the six standard geographic subareas used for analytical purposes: Nova Scotia, Gulf of Maine, Georges Bank, Georges Slope, Southern New England Shelf, and Southern New England Slope.

(1966); Schopf (1967); and Schopf and Colton (1966); and Mountain and Holzwarth (1989).

Sediment Organic Carbon

Organic carbon in bottom sediments was measured by gasometric method in samples after removal of $CaCO_3$ by acid treatment. Data are contained in Hathaway (1971).

Description of the Region

Topography

Relief of the sea bottom off the New England region has been studied most recently by the U.S. Geological Survey and the Woods Hole Oceanographic Institution (Austin et al., 1980; Emery, 1965a, 1966b; Emery and Ross, 1968; Emery and Uchupi, 1972; Gibson et al. 1968; Klitgord and Behrendt, 1979; Klitgord et al., 1982. Schlee et al., 1976; Sheridan, 1974; Uchupi, 1965b, 1966a, 1966b, 1966c, 1968; Uchupi and Emery, 1967; Uchupi et al., 1977; Uchupi and Austin, 1979; Valentine, 1981). Figure 6 is based on, and has been derived from, a much larger more detailed chart by Uchupi (1965a), U.S.G.S. Map I-451, scale 1:1,000,000.

Topographically, the New England offshore area consists of several large, grossly different geological features. The largest and most complex feature is the Gulf of Maine, an immense, nearly oval-shaped glacially eroded depression on the continental shelf. The topography in this depression is very irregular, resulting in numerous basins separated by ridges, swales, and banks. These topographic irregularities are due in part to deposition, gouging, erosion, and related actions during the Pleistocene period of glaciation. Greatest depth in the gulf is 377 m, in Georges Basin; shallowest offshore depth in the gulf is 9 m, at Amen Rock on Cashes Ledge in the west central part of the Gulf of Maine (see Ballard and Uchupi, 1975; Austin et al., 1980; Klitgord et al., 1982; Schlee et al., 1976).

Georges Bank is another striking topographic feature. It is an enormous (120 km by 240 km) submarine cuestalike bank situated at the mouth of the Gulf of

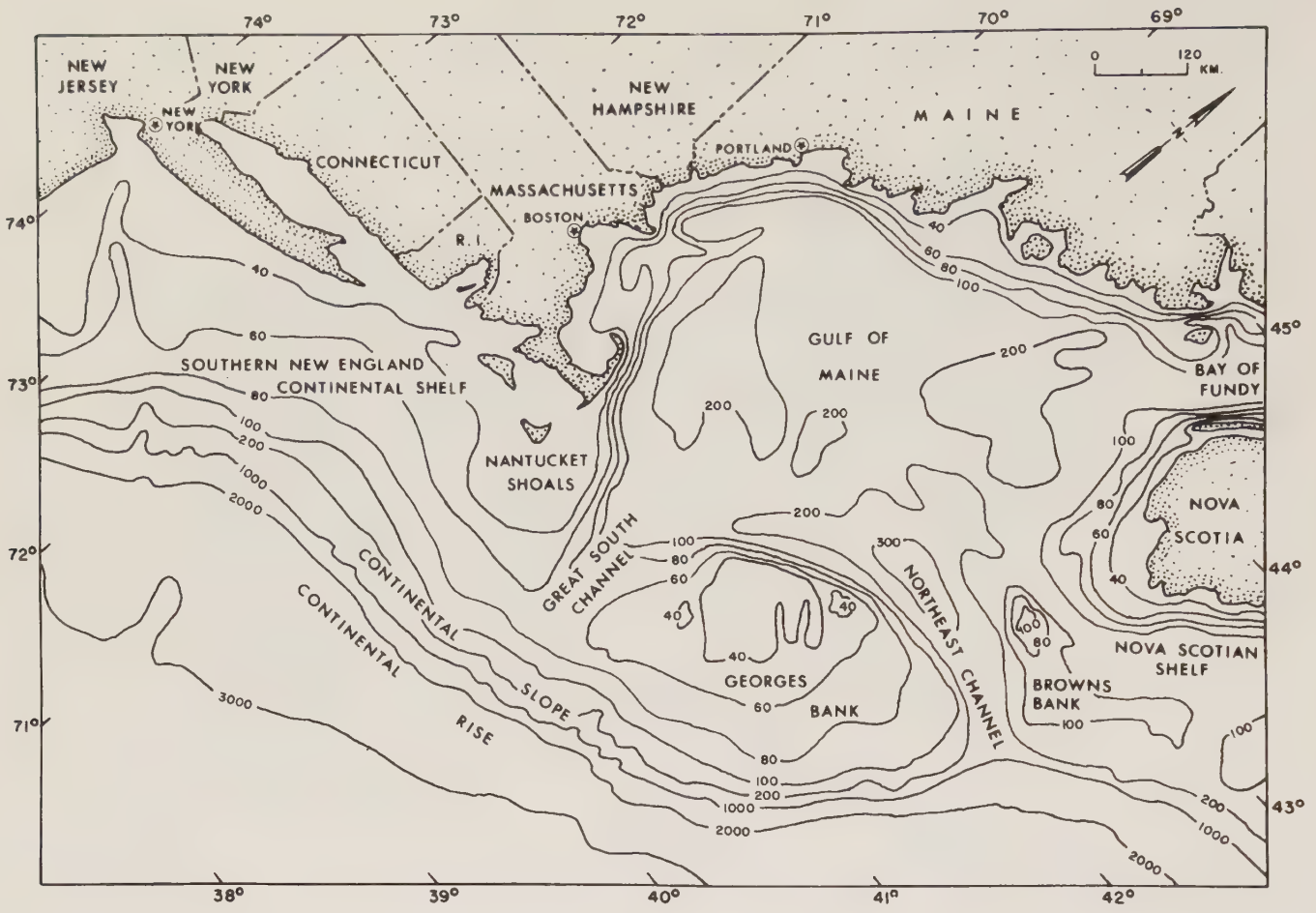

Figure 6

Chart of the study area showing bathymetric and geographical features. Depth contours are in meters (adapted from Uchupi 1965).

Maine. The bank slopes gently to the southeast and south and its surface is relatively smooth except for a series of sand ridges in the shallow northwest and north-central sections. The sand ridges are formed by exceptionally strong tidal currents that prevail in this region. Tidal currents generally flow with greatest velocity in the northwest and southeast directions. Further details relating to Georges Bank are contained in Emery and Uchupi (1965); Uchupi et al. (1977); Valentine (1981); Butman (1982, 1987); Butman et al. (1982, 1987); Backus (1987); Bourne (1987); Butman and Beardsley (1987); Cohen and Grosslein (1987); Cooper et al. (1987); Emery (1987); Flagg (1987); Howart (1987); Klitgord and Schlee (1987); Maciolek and Grassle (1987); Michael (1987); Neff (1987); Twichell et al. (1987); Uchupi and Austin (1987).

Nantucket Shoals is a relatively shallow and topographically uneven area southeast of Nantucket Island, Massachusetts. Principal irregularities are large swales and ridges extending in north-south and northeast-southwest directions.

The southern New England continental shelf is a gently seaward-sloping region with rather smooth topography. Width of the shelf is approximately 100 km and the shelf break occurs at a depth of about 120 m. See Garrison and McMaster (1966) for more details.

The continental slope is a narrow zone along the outer margin of the shelf extending from the shelf break to a depth of 2,000 m. This zone has a comparatively steep gradient, but less than 5°, and the relief is moderately smooth except where it is cut by submarine canyons. The continental rise (2,000–6,000 m) is generally similar to the slope in having only gradual changes in surficial topography. However, the overall gradient is substantially less than that for the continental slope. Consult Emery (1965a), Emery and Ross (1968), Gibson et al. (1968), Schlee et al. (1979), Sheridan (1974), and Uchupi et al. (1977) for details of topography of this region.

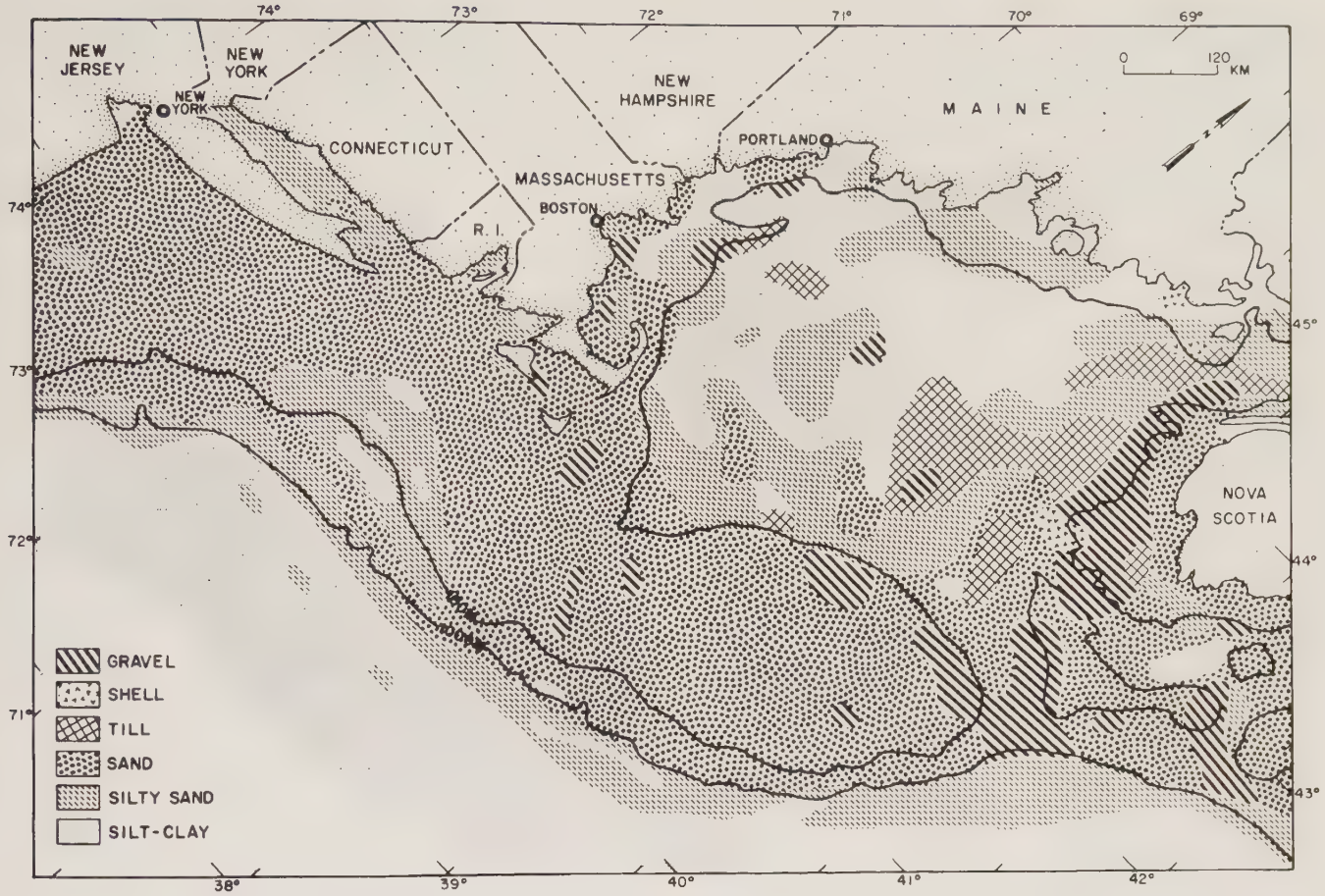

Figure 7
Geographical distribution of bottom-sediment types in the study area.

Bottom Sediments

The composition of sediments blanketing the sea floor throughout the study area is well known. Detailed studies have included sedimentological aspects of general lithology, particle size composition, calcium carbonate content, organic carbon content, nitrogen content, minerology, sand and gravel fractions, and other components. A representative selection of publications dealing with the bottom sediments of New England marine waters includes: Shepard, et al. (1934); Shepard and Cohee (1936); Stetson (1936, 1938, 1949); Shepard (1939); Hough (1940, 1942); Wigley (1961a); Uchupi (1963, 1965b, 1966a, 1966b, 1966c, 1968, 1969); Emery (1965a, 1965b, 1966a, 1966b, 1968); Emery et al. (1965); Rvachev (1965); Garrison and McMaster (1966); Hülsemann (1966, 1967); McMaster and Garrison (1966); Ross (1967, 1970a, 1970b); Uchupi and Emery (1967); Emery and Ross (1968); Schlee (1968, 1973); Schlee and Pratt (1970); Emery and Uchupi (1972); Trumbull (1972); Milliman (1973); Wigley and Stinton (1973); Sheridan (1974); Austin et al. (1980); Twichell et al. (1981); Butman (1982, 1987); Klitgord et. al. (1982); and Valentine et al. (1980).

Relict glacial sediments are the major constituents covering most of the study area, particularly on the continental shelf. Quartz and feldspar sands and granite and gneiss gravels are particularly common in the shallower areas and on the topographically high elevations in deeper water. Fine-textured sediments, mainly silts and clays, that mantle the continental slope, continental rise, and protected pockets and basins on the continental shelf are predominantly present-day detrital sediments.

Large areas in the deeper part of the Gulf of Maine are floored with unsorted glacial till, whereas the shallow banks and ridges are commonly covered with gravel or sand of glacial origin that remained after washing action removed the finer particles. In some deep parts of the Gulf, where water currents are minimal, the till is overburdened with layers of silt and clay. In Long Island Sound, Buzzards Bay, and many of the smaller bays along the coast, the sediments are composed largely of silts and clays, with sand and gravel common in the nearshore zones.

The sediment chart prepared for this report (Fig. 7) is based on sediment samples taken from the same grab hauls from which the fauna was obtained.

Sediment organic carbon

The distribution of organic carbon in the bottom sediments of the region is depicted in Figure 8. Values for sediment organic carbon content from samples were low to moderate, ranging from less than 0.5% to slightly over 7% (7.04). The major portion of the continental shelf contains small amounts (< 0.5%) of organic carbon in sediments, with only small, discrete patches, especially in the Southern New England shelf area, of slightly greater amounts (0.5–1.99%). Organic carbon content of sediments in the two slope subareas, Georges Slope and Southern New England Slope, was somewhat higher than on the shelf with values between 0.50 and 0.99% prevailing and with small areas on the Southern New England slope containing from 1.00 to 1.99% organic carbon. The sediments in both the Gulf of Maine and Long Island Sound contain comparatively larger amounts of carbon, primarily in the 1.00 to 1.99% range over most of their respective areas. Highest organic carbon content (from 2.00 to 7.04%) was almost exclusively restricted to the major embayments and estuaries within the study area; only offshore exceptions to this were two small areas on Stellwagen Bank and in the area known as Georges Basin, where organic carbon contents in that range were found.

Hydrography

A substantial amount of information has been amassed over the years concerning the hydrography of the offshore New England region. Some of the first hydrographic data collected were temperature measurements taken by Benjamin Franklin's nephew in 1789. Since that time numerous studies have been conducted primarily by government organizations, such as the U.S. Fish Commission (subsequently named the U.S. Bureau of Commercial Fisheries, and currently called the National Marine Fisheries Service), the U.S. Coast Survey (now the National Ocean Survey), U.S. Coast Guard, Tidal Survey of Canada, Biological Board of Canada (Fisheries Research Board of Canada), coastal states organizations, Bigelow Laboratory, Woods Hole Oceanographic Institution, Harvard University, Massachusetts Institute of Technology, University of

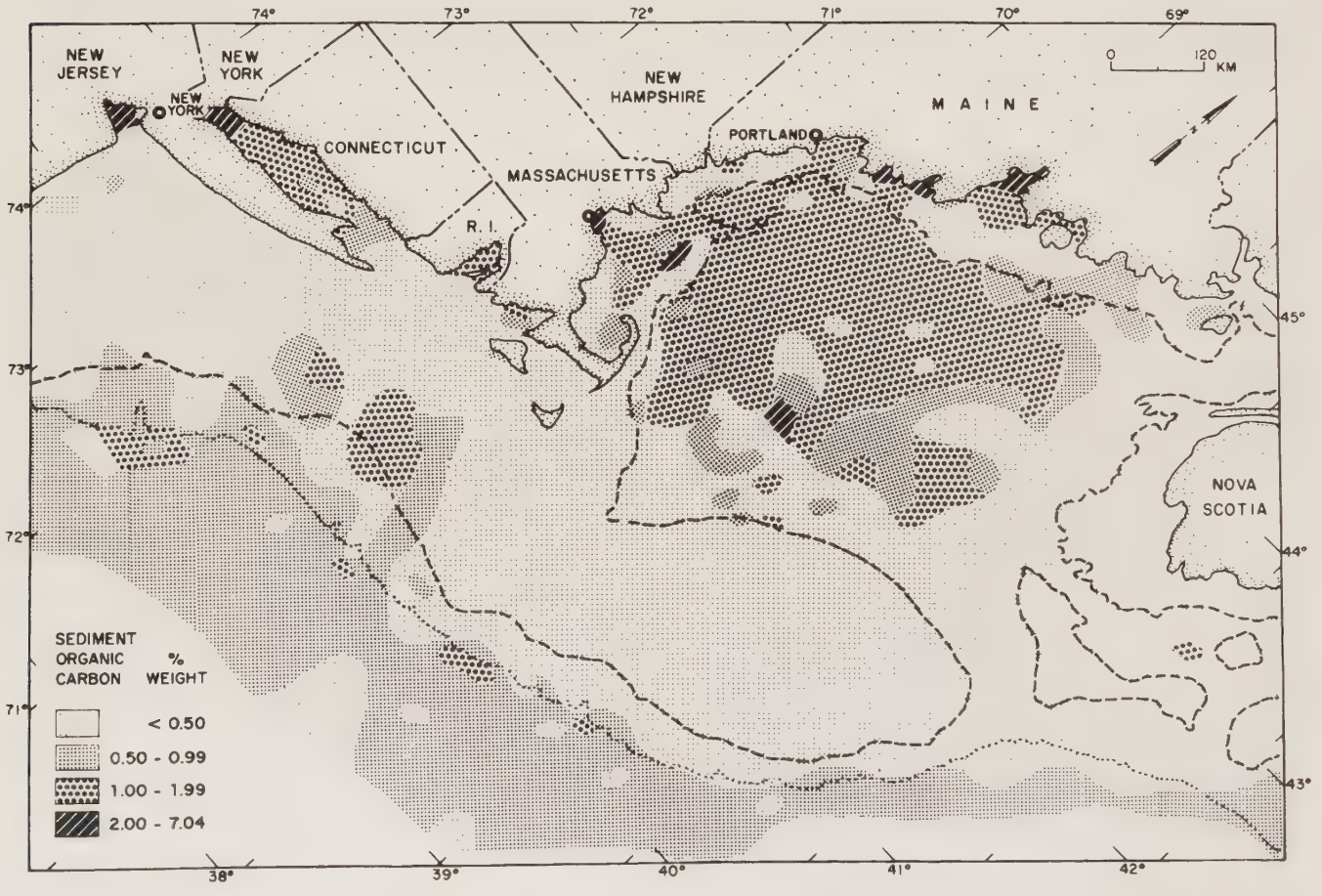

Figure 8
Geographic distribution of organic carbon in the bottom sediments.

Rhode Island, and other private and governmental organizations.

One of the most comprehensive reports on this subject is the monograph entitled "Physical Oceanography of the Gulf of Maine" by Henry B. Bigelow (1927). He describes the essential features of water temperature, salinity, tidal and nontidal circulation, and seasonal variation in these hydrographic features. Much detailed information was added in succeeding years particularly by John B. Colton and his associates at the Bureau of Commerical Fisheries Biological Laboratory at Woods Hole, Massachusetts, and by Dean F. Bumpus and his colleagues at the Woods Hole Oceanographic Institution (Stetson, 1937; Bumpus, 1960, 1961; Colton, 1964; Bumpus and Lauzier, 1965; Bumpus et al., 1973; Butman et al., 1980, 1982; Dorkins, 1980; Ramp et al., 1980, Moody et. al., 1984, Mountain and Holzwarth, 1989, among others). Discussions of early oceanographic research in this region and references to the literature are given by Colton (1964), Schopf (1968a), and Wright (1987).

In brief, the main features pertaining to water circulation in the study area are as follows: 1) cold water on the Nova Scotian Shelf flows southwestwardly along that feature and turns northward into the Gulf of Maine; 2) Gulf of Maine waters form a large nontidal counterclockwise gyre; 3) waters overlying Georges Bank form a clockwise gyre; 4) nontidal currents generally flow southwestwardly and westward across Nantucket Shoals and on the Southern New England continental shelf; 5) freshwater runoff from land empties by means of large New England and Canadian rivers into the northern and western sections of the study area; 6) incursions of relatively warm high-salinity slope water enter the Gulf of Maine by way of Northeast Channel; 7) tidal amplitude is exceptionally large in the Bay of Fundy region, and tidal currents are strong throughout the entire New England continental shelf area; 8) the Gulf Stream flows northeastward in deep water south of the New England continental shelf (usually the Gulf Stream's northern edge is more than one hundred miles south of the continental shelf in the region south of Nantucket Island); and 9) below the Gulf Stream in the vicinity of the ocean bottom, the Western Boundary Current flows southwestwardly.

Oceanic waters in the vicinity of the Gulf Stream maintain a relatively constant salinity of about 35‰. Most of the waters overlying the continental shelf have a salinity range from 32 to 34‰. Salinity of inshore waters, which are more strongly influenced by runoff, fluctuate seasonally and drop to 28‰ in late spring when river discharge is maximum.

Temperature of water in deep oceanic areas beyond the continental shelf is typically homostenothermal. Waters are warm (20°C) at the surface and cold at the bottom (2.5 to 5°C), and both surface and bottom temperatures remain relatively stable throughout the year. Conversely,the inshore waters along the coast are characteristically heteroeurythermal. They are cold (0°C) in winter and warm in summer, and because of the shallowness and general turbulence of the water, the temperature differential between surface and bottom is relatively small. Also, there is considerable latitudinal effect on inshore waters; in southern areas the temperature does not drop as low in winter and rises higher in summer than it does in northern areas. Midshelf waters—those between the oceanic and inshore zones—are generally intermediate in their temperature regime. Temperature diversity between the surface and bottom is moderate. Seasonal changes in temperature are greater in offshore shallow areas (such as Nantucket Shoals and Georges Bank) than in basins and other deep water areas, but the range is less than that in coastal waters. Annual fluctuation in temperature of bottom water is considerably less than that of surface waters. Latitudinal effect on shelf water masses is pronounced; Nova Scotian water is substantially colder than other water masses within the study area, and the temperature generally increases to the west and south (Bigelow, 1933; McLellan, 1954; Edwards et al., 1962; Colton et al., 1968; Schopf and Colton, 1966; Schopf, 1967; Colton, 1968a, 1968b, 1969; Colton and Stoddard, 1972, 1973; Mountain and Holzwarth, 1989; Colton et al.[10]; Colton et al.[11]; Colton et al.[12]; Colten et al.[13]).

Thermal extremes, rather than means, are believed to have a marked influence on the presence or absence of various kinds of benthic animals. In order to detect the possible influence of thermal extremes as a limiting factor, we have analyzed the invertebrate fauna distribution in relation to the approximate annual minimum and maximum water temperatures, and the range in water temperature, to which the various taxa are

[10] Colton, J. B., Jr., R. R. Marak, and S. R. Nickerson. 1965a. Environmental observations on continental shelf Nova Scotia to Long Island, March 1965, *Albatross IV* cruise 65-3. U.S. Bur. Commer. Fish. Biol. Lab. Woods Hole, Mass., Lab. Ref. 65-15, 3 p., 9 figs. (mimeo). Unpubl. manuscript.

[11] Colton, J. B., Jr., R. R. Marak, and S. R. Nickerson. 1965b. Environmental observations on continental shelf Nova Scotia to Long Island, September 1965, *Albatross IV* cruise 65-12. U.S. Bur. Commer. Fish. Biol. Lab. Woods Hole, Mass., Lab. Ref. 65-19, 3 p., 9 figs. (mimeo). Unpubl. manuscript.

[12] Colton, J. B., Jr., R. R. Marak, and S. R. Nickerson. 1966a. Environmental observations on continental shelf Nova Scotia to Long Island, March 1966, *Albatross IV* cruise 66-2. U.S. Bur. Commer. Fish. Biol. Lab. Woods Hole, Mass., Lab. Ref. 66-6, 3 p., 10 figs. (mimeo). Unpubl. manuscript.

[13] Colton, J. B., Jr., R. R. Marak, S. R. Nickerson, and R. R. Stoddard. 1966b. Environmental observations on continental shelf Nova Scotia to Long Island, May–June 1966. *Albatross IV* cruise 66-7. U.S. Bur. Commer. Fish. Biol. Lab., Woods Hole, Mass., Lab. Ref. 66-7, 3 p., 10 figs. (mimeo). Unpubl. manuscript.

subjected. Charts were constructed to illustrate the isotherms of maximum bottom water temperature (Fig. 9) minimum bottom water temperature (Fig. 10), and annual range in bottom water temperature (Fig. 11). Data for these charts were extracted from temperature records taken during the sampling period when biological data were collected, August 1956 through August 1965, and from the literature (see above citations). Temperature patterns depicted in these charts are intended to provide a general scheme of annual temperature change. Higher or lower temperatures may have existed for short periods in some areas and may have been missed because of the opportunistic nature of the sampling. Extremes of this kind, however, are not considered usual or of great magnitude.

These charts disclose a wide annual temperature range in coastal bays and in shallow offshore areas, such as Georges Bank and Nantucket Shoals. Very little change occurs in deep water. At depths below 500 meters the annual variation in temperature is roughly 0–3.9°C. Bottom water in the Gulf of Maine is relatively cold, 4 to 8°C and changes very little throughout the year. Bottom water on the Scotian Shelf and Browns Bank is particularly cold in the spring and warms up only to moderate levels in the fall and early winter. Annual average temperature of bottom water for some of the major areas calculated by Schopf and Colton (1966) and Schopf (1967) are: Georges Bank 8.6°C, Nantucket Shoals 7.8°C, Gulf of Maine 5.7°C, Browns Bank 5.0°C, and the Nova Scotian Shelf 4.6°C.

Zoogeography

The topographic, hydrographic, climatic, and faunal complexities of the sublittoral portion of the study area cause considerable difficulty in the definition of definitive zoogeographic boundaries in the Northwest Atlantic. Until recently, the traditional view among biogeographers was that the region embraced portions of two major zoogeographic provinces: 1) The Boreal Province, sometimes referred to as Acadian or Nova Scotian, which extends from Newfoundland to Cape Cod, and 2) The Trans-Atlantic or (Warm Temperate) Province

Figure 9
Distribution of maximum reported bottom water temperatures (in degrees Celsius) in the study area.

of which the Virginian subprovince extends from Cape Cod southward to Cape Hatteras (Ekman, 1953; Hedgpeth, 1957). Although these views postulated the highly visible physical features of Cape Cod and Cape Hatteras as the boundaries between these provinces (a credible hypothesis topographically and hydrographically), no definitive consensus of opinion among biogeographers of the period prevailed as to the precise placement of the boundaries in the Northwest Atlantic. Indeed, the plethora of varying definitions and terms led to a rather confusing semantic problem that exists to this day. Further, these views resulted from studies based almost solely on biological and physical data from inshore or nearshore areas.

Hazel (1970) reviewed the historical development of faunal provinces for North America and Europe based on the work of 17 authors from 1838 to 1966 and noted that during that period essentially three biogeographic schemes evolved to characterize the Northwest Atlantic down to Cape Hatteras: 1) Cape Cod acts as a boundary between the cold temperate Nova Scotian or Boreal Province to the north, and the warm temperate Virginian subprovince to the south, with Cape Hatteras forming the boundary between the Virginian and Carolinian subprovinces, which together formed the Trans-Atlantic Province down to present day Cape Kennedy; 2) a region of overlap or transition, lacking a unique fauna of its own (low endemism) with no provincial status, between the Nova Scotian and Carolinian Provinces; and 3) A cold temperate Boreal Province extending from Newfoundland to Cape Hatteras.

Although more recent biogeographic studies, based mostly on offshore fauna within the region, such as those of Bousfield (1960), Coomans (1962), Schopf (1968b), Franz (1970), Hazel (1970), Bousfield (1973), Franz (1975), Bowen et al. (1979), Kinner (1978), Watling (1979), Franz and Merrill (1980a, 1980b), and Franz et al. (1981) have expressed concern over the boundary's existence and have attempted to resolve the semantic problem of terminology through revision and simplification, they have not, for the most part, significantly altered the three biogeographic concepts of earlier workers. These recent works, however, have provided some new insights concerning the placement of

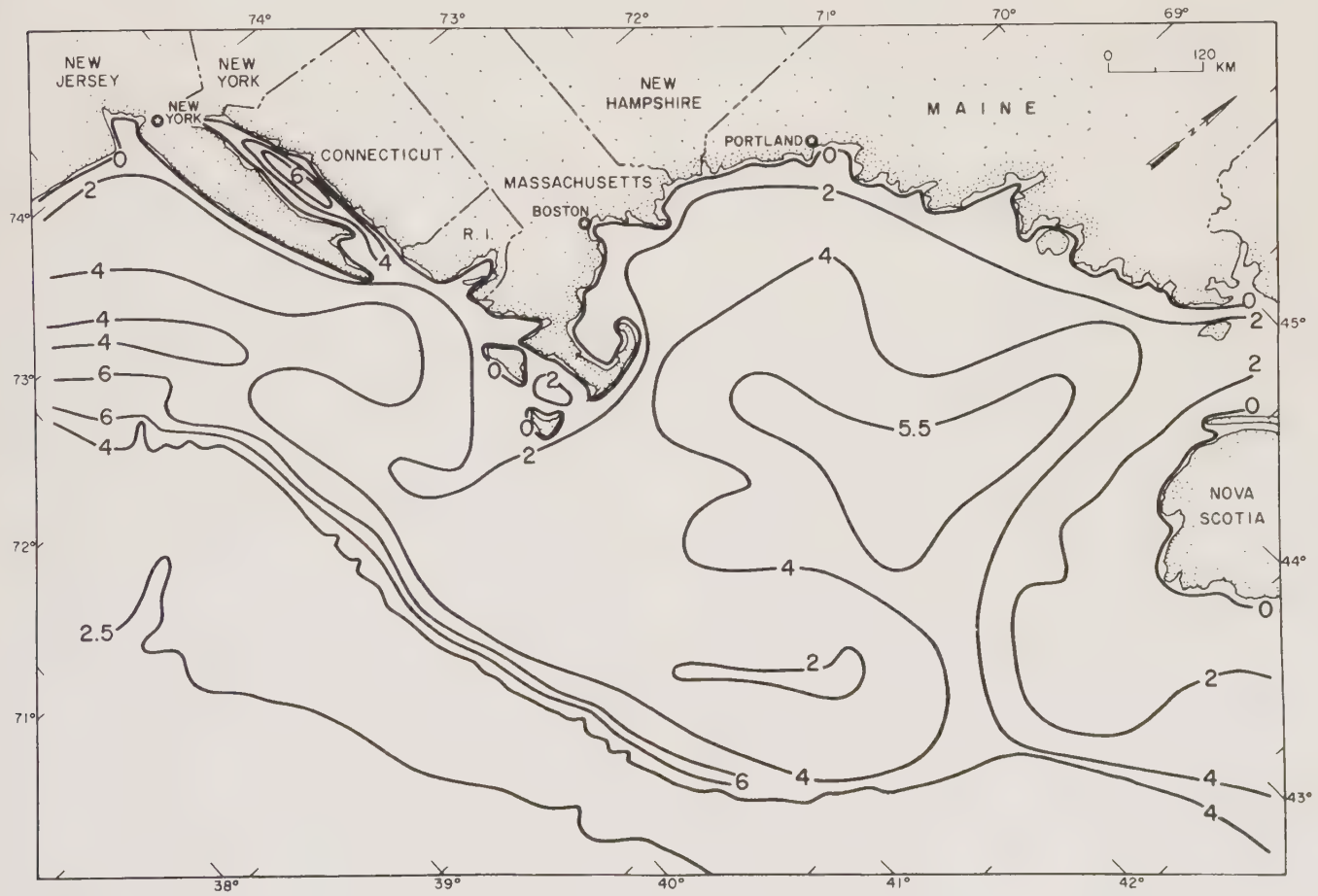

Figure 10
Distribution of minimum reported bottom water temperatures (in degrees Celsius) in the study area.

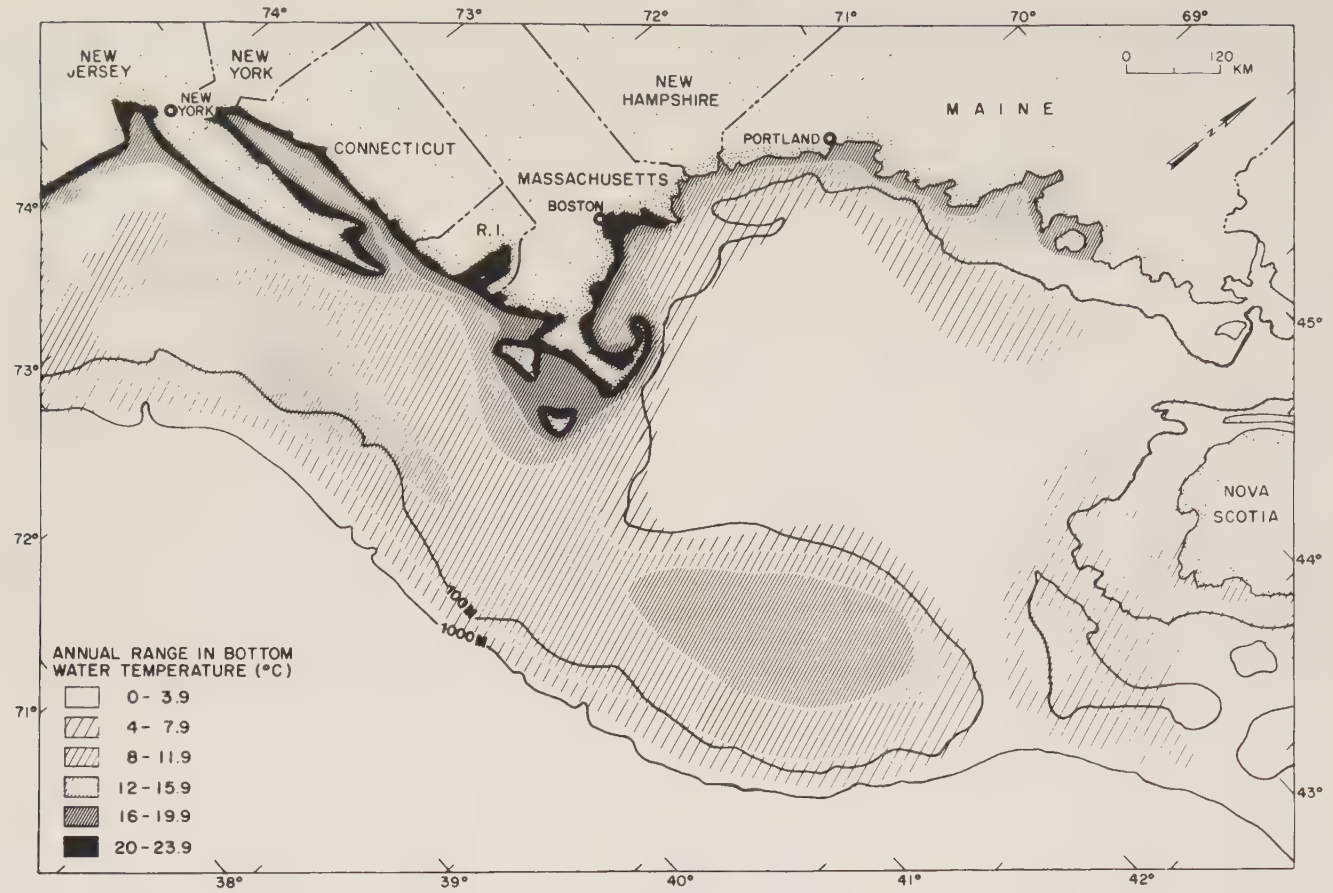

Figure 11

Distribution of the annual range (difference between maximum and minimum reported values) in bottom water temperature (in degrees Celsius) in the study area.

more meaningful zoogeographic boundaries for regulating the distribution of benthic taxa within the region.

Boundaries of the geographical area considered in this report were purposely selected so that they did not terminate at the margin of a perceived zoogeographical barrier. Cape Cod, lying roughly in the center of the study area, is of course the main physical feature historically considered to mark the separation between the Boreal and Trans-Atlantic Provinces. The recent work of Schopf (1968b), Hazel (1970), Watling (1979b), Franz et al. (1981), and other reports (Wigley and Burns, 1971; Williams and Wigley, 1977; Theroux and Wigley, 1983; and Theroux and Grosslein, 1987) based on the same data as, and including, the present report corroborate the fact that Cape Cod is indeed a zoogeographic boundary. However, the seaward extension of this boundary, at least as it pertains to benthic animals, does not traverse the continental shelf over Nantucket Shoals and the southwestern terminus of Great South Channel as previously supposed. Rather, the boundary appears to lie along an easterly path across the northern end of Great South Channel at depths of 50 to 100 m and to continue along the northern margin of Georges Bank and thence southeasterly along the western boundary of Northeast Channel.

In bathyal and abyssal depths there are at least two other zoogeographic provinces. Along the continental slope, at depths between 150 and 2,000 m, is the Atlantic Transitional Province (Cutler, 1977), and at depths between 2,000 and 4,000 m is the Atlantic Bathyal-Abyssal Province. Because of the interdigitating distributional patterns resulting from the southward submergence of Boreal species and the ascendency of Transitional and Bathyal-Abyssal species in their northward extension, the delineation of these provinces is imprecise and only partially aligned with topographic features.

A great deal more work of a zoogeographic nature on the many remaining unstudied taxa of benthic invertebrates inhabiting the area needs to be performed before precise zoogeographic boundaries may be drawn, if at all possible.

Faunal Composition

The macrobenthic invertebrate fauna of the New England region is moderate in variety. A modest number of species (567 in the present study), in combination with a graded abundance of individuals composed of a variety of dominants and codominants, is characteristic of the fauna, and is generally typical of Boreal-Temperate faunal assemblages.

Taxa reported on in this study represent 13 phyla and 28 lesser groups such as subphyla, classes, subclasses, and orders. The majority of species are Boreal forms, followed closely in abundance by Virginian (or warm-temperate) forms. Additionally, there is a small contingent of Arctic and Subarctic species, particularly in the Gulf of Maine. Also, a few tropical and subtropical species occur chiefly in the Southern New England and Georges Bank areas.

The ecological importance of these groups, judged primarily from their numerical abundance and biomass, ranges from minor (components that account for less than 0.1% in number of individuals and biomass) to dominant components that make up 20% or more in number of individuals or biomass. The 44 major taxonomic groups, with the percentage of total number of individuals and percentage of total biomass for each, are listed in Table 3. Also, they are classified into four dominance categories, I to IV.

Over 80% of both the biomass and number of individuals in the macrobenthos is formed by only five taxonomic groups. These are classified in dominance category I in Table 3. Bivalvia is the dominant contributor (44.1%) to the biomass and is also a major component (10.8%) in terms of numbers of individuals. Amphipoda, on the other hand, is numerically dominant (43.4%) but contributes only 2.3% of the biomass. Conversely, Echinoidea and Holothuroidea are important components of the biomass, but are numerically sparse. Annelida is a major contributor in both measures of quantity.

Category II, in Table 3, consists of eight taxa that contribute moderate biomass (1.2 to 2.3% of the total fauna) and number of individuals (1.0 to 2.9% of the total fauna). Categories III and IV contain those taxa that contribute small to very small quantities to the total biomass and density.

The New England region macrobenthos is dominated by members of four phyla: Annelida, Mollusca, Arthropoda, and Echinodermata. These groups will be discussed in more detail in the following sections. Table 4 lists the components of the macrobenthic invertebrate fauna inhabiting the New England region, and Table 5 lists the quantitative measures of abundance (mean and total weights and numbers per square meter), number of samples, and frequency of occurrence for each taxonomic group considered in this report.

Table 3

Rank order of major taxonomic groups according to percentage composition of the total macrobenthic fauna in terms of biomass and number of specimens.

Dominance category	Taxa	Percentage of total biomass	Taxa	Percentage of total number specimens
I	Bivalvia	44.1	Amphipoda	43.4
	Echinoidea	20.0	Annelida	28.1
	Annelida	9.5	Bivalvia	10.8
	Holothuroidea	7.0		
	Total	80.6	Total	82.3
II	Zoantharia	3.5	Ophiuroidea	2.9
	Amphipoda	2.3	Echinoidea	1.9
	Ascidiacea	2.2	Cumacea	1.7
	Cirripedia	1.9	Zoantharia	1.5
	Ophiuroidea	1.8	Cirripedia	1.5
	Gastropoda	1.2	Gastropoda	1.2
	Asteroidea	1.2	Ascidiacea	1.1
	Porifera	1.2	Bryozoa	1.0
	Total	15.3	Total	12.8
III	Decapoda	0.8	Isopoda	0.8
	Bryozoa	0.7	Nemertea	0.5
	Brachiopoda	0.5	Decapoda	0.5
	Nemertea	0.4	Hydrozoa	0.4
	Sipunculida	0.4	Sipunculida	0.4
	Hydrozoa	0.3	Brachiopoda	0.3
	Scaphopoda	0.2	Scaphopoda	0.3
	Echiura	0.2	Holothuroidea	0.3
	Isopoda	0.2	Nematoda	0.2
	Alcyonaria	0.1	Mysidacea	0.2
	Polyplacophora	0.1	Porifera	0.1
	Cumacea	0.1	Alcyonaria	0.1
			Polyplacophora	0.1
			Asteroidea	0.1
	Total	4.0	Total	4.3
IV	Turbellaria	<0.1	Turbellaria	<0.1
	Priapulida		Priapulida	
	Nematoda		Cephalopoda	
	Cephalopoda		Echinoidea	
	Arachnida		Arachnida	
	Pycnogonida		Pycnogonida	
	Ostracoda		Ostracoda	
	Copepoda		Copepoda	
	Mysidacea		Tanaidacea	
	Tanaidacea		Crinoidea	
	Crinoidea		Pogonophora	
	Pogonophora		Hemichordata	
	Hemichordata		Echiura	
	Total	<1.0	Total	<1.0

Table 4
List of macrobenthic invertebrate species contained in quantitative samples obtained within the study area.

PORIFERA
- Demospongiae
  - Hadromerida
    - Suberitidae
      - *Polymastia* sp.

COELENTERATA
- Hydrozoa
  - *Hydractinia echinata* Fleming, 1828
  - *Hydractinia* sp.
- Anthozoa
  - Alcyonaria
    - Alcyonacea
      - *Alcyonium* sp.
    - Gorgonacea
      - *Acanella* sp.
      - *Paragorgia arborea* (Linnaeus, 1767)
      - *Primnoa reseda* (Pallas, 1766)
    - Pennatulacea
      - *Pennatula aculeata* Danielssen and Koren, 1858
      - *Pennatula* sp.
      - *Stylatula elegans* (Danielssen, 1860)
  - Zoantharia
    - Zoanthidea
      - *Epizoanthus incrustatus* (Verrill, 1864)
      - *Epizoanthus* sp.
  - Actiniaria
    - *Tealina felina* (Linnaeus, 1767)
    - *Edwardsia sulcata* (T. Pennant, 1777)
    - *Edwardsia* sp.
    - *Actinostola callosa* Verrill, 1882
    - *Antholoba perdix* (Verrill, 1882)
  - Madreporaria
    - *Astrangia* sp.
    - *Flabellum goodei* Verrill, 1878
    - *Flabellum* sp.
  - Ceriantheria
    - *Cerianthus borealis* Verrill, 1878
    - *Cerianthus* sp.
    - *Ceriantheopsis americanus* Verrill, 1866

Annelida
- Polychaeta
  - Amphinomida
    - Amphinomidae
      - *Paramphinome jeffreysii* (McIntosh, 1868)
  - Capitellida
    - Capitellidae
      - *Capitella* sp.
    - Maldanidae
      - *Asychis biceps* (Sars, 1861)
      - *Maldane* sp.
  - Cossurida
    - Cossuridae
      - *Cossura longicirrata* Webster and Benedict, 1883
      - *Cossura* sp.
  - Eunicida
    - Arabellidae
      - *Arabella iricolor* (Montagu, 1804)
      - *Arabella* sp.
      - *Drilonereis longa* Webster, 1879
      - *Drilonereis* sp.
      - *Notocirrus* sp.
    - Eunicidae
      - *Eunice pennata* (Müller, 1776)
      - *Eunice* sp.
      - *Marphysa* sp.
    - Lumbrineridae
      - *Lumbrinerides acuta* (Verrill, 1875)
      - *Lumbrineris fragilis* (Müller, 1776)
      - *Lumbrineris* sp.
      - *Ninoe* sp.
    - Onuphidae
      - *Diopatra cuprea* (Bosc, 1802)
      - *Diopatra* sp.
      - *Hyalinoecia tubicola* (Müller, 1776)
      - *Hyalinoecia* sp.
      - *Nothria conchylega* Sars, 1835
      - *Onuphis eremita* Audoin and Milne-Edwards, 1833
      - *Onuphis opalina* (Verrill, 1873)
      - *Onuphis quadricuspis* Sars, 1872
      - *Onuphis sp.*
      - *Paradiopatra* sp.
  - Flabelligerida
    - Flabelligeridae
      - *Brada* sp.
      - *Flabelligera* sp.
      - *Pherusa* sp.
  - Opheliida
    - Opheliidae
      - *Ophelia* sp.
      - *Ophelina aulogaster* (H. Rathke, 1843)
      - *Ophelina* sp.
      - *Travisia carnea* Verrill, 1873
      - *Travisia* sp.
    - Scalibregmidae
      - *Scalibregma inflatum* Rathke, 1843
      - *Scalibregma* sp.
  - Orbiniida
    - Orbiniidae
      - *Orbinia ornata* (Verrill, 1873)
      - *Orbinia swani* Pettibone, 1957
      - *Orbinia* sp.
      - *Scoloplos robustus* (Verrill, 1873)
      - *Scoloplos* sp.
      - *Aricidea jeffreysii* (McIntosh, 1879)
      - *Aricidea* sp.
    - Paraonidae
      - *Paraonis* sp.
  - Oweniida
    - Oweniidae
      - *Owenia fusiformis* delle Chiaje, 1844
      - *Owenia* sp.
  - Phyllodocida
    - Aphroditidae
      - *Aphrodita hastata* Moore, 1905
      - *Aphrodita* sp.
      - *Laetmonice* sp.
    - Glyceridae
      - *Glycera americana* Leidy, 1855
      - *Glycera capitata* Oersted, 1843
      - *Glycera dibranchiata* Ehlers, 1868
      - *Glycera* sp.

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Table 4 (continued)

- Goniadidae
  - *Goniada maculata* (Oersted, 1843)
  - *Goniada* sp.
  - *Goniadella* sp.
  - *Ophioglycera gigantea* Verrill, 1885
  - *Ophioglycera* sp.
- Hesionidae
  - *Nereimyra punctata* (O.F. Müller, 1776)
- Nephtyidae
  - *Aglaophamus circinata* (Verrill, 1874)
  - *Aglaophamus* sp.
  - *Nephtys bucera* Ehlers, 1869
  - *Nephtys incisa* Malmgren, 1865
  - *Nephtys picta* Ehlers, 1868
  - *Nephtys* sp.
- Nereidae
  - *Ceratocephale loveni* Malmgren, 1867
  - *Ceratocephale* sp.
  - *Nereis* sp.
- Phyllodocidae
  - *Eteone* sp.
  - *Eumida sanguinea* (Oersted, 1843)
  - *Phyllodoce arenae* Webster, 1879
  - *Phyllodoce* sp.
- Pilargiidae
  - *Ancistrosyllis* sp.
- Polynoidae
  - *Harmothoe* sp.
  - *Lepidonotus squamatus* (Linnaeus, 1758)
- Sigalionidae
  - *Leanira* sp.
  - *Pholoe minuta* (Fabricius, 1780)
  - *Sigalion arenicola* Verrill, 1879
  - *Sigalion* sp.
- Sphaerodoridae
  - *Sphaerodorum gracilis* (Rathke, 1843)
- Syllidae
  - *Exogone verugera* (Clarapede, 1868)
  - *Exogone* sp.
- Tomopteridae
  - *Tomopteris* sp.

Sabellida
- Sabellidae
  - *Chone infundibuliformis* Krøyer, 1856
  - *Chone* sp.
  - *Euchone* sp.
  - *Potamilla neglecta* (Sars, 1850)
  - *Potamilla reniformis* (Linnaeus, 1788)
  - *Potamilla* sp.
  - *Sabella* sp.
- Serpulidae
  - *Filograna* sp.
- Spirorbidae
  - *Spirorbis* sp.

Spionida
- Chaetopteridae
  - *Spiochaetopterus* sp.
- Cirratulidae
  - *Chaetozone* sp.
  - *Cirratulus* sp.
  - *Tharyx* sp.
- Spionidae
  - *Diospio uncinata* Hartman, 1951
  - *Laonice cirrata* (Sars, 1851)
  - *Laonice* sp.
  - *Polydora concharum* Verrill, 1880
  - *Polydora* sp.
  - *Priospio* sp.
  - *Spio setosa* Verrill, 1873
  - *Spio* sp.
  - *Spiophanes bombyx* (Clarapede, 1870)

Sternaspida
- Sternaspidae
  - *Sternaspis scutata* (Renier, 1807)
  - *Sternaspis* sp.

Terebellida
- Ampharetidae
  - *Ampharete acutifrons* (Grube, 1860)
  - *Ampharete* sp.
  - *Melinna cristata* (Sars, 1851)
  - *Melinna* sp.
- Pectinariidae
  - *Pectinaria gouldii* (Verrill, 1873)
  - *Pectinaria* sp.
- Terebellidae
  - *Amphitrite* sp.
  - *Streblosoma spiralis* (Verrill, 1874)
  - *Steblosoma* sp.

POGONOPHORA
- Siboglinidae
  - *Siboglinum angustum* Southward and Brattegard, 1968
  - *Siboglinum atlanticum* Southward and Southward, 1958
  - *Siboglinum ekmani* Jagerston, 1956
  - *Siboglinum holmei* Southward ,1963
  - *Siboglinum pholidotum* Southward and Brattegard, 1968
  - *Siboglinum* sp.
- Polybrachiidae
  - *Crassibranchia sandersi* Southward, 1968
  - *Diplobrachia similis* Southward and Brattegard, 1968
  - *Polybrachia* sp.

SIPUNCULIDA
- *Aspidosiphon zinni* Cutler, 1969
- *Golfingia catharinae* (Müller, 1789)
- *Golfingia elongata* (Keferstein, 1869)
- *Golfingia eremita* (Sars, 1851)
- *Golfingia flagrifera* (Selenka, 1885)
- *Golfingia margaritacea* (Sars, 1851)
- *Golfingia minuta* (Keferstein, 1865)
- *Golfingia murinae murinae* Cutler, 1969
- *Onchnesoma steenstrupi* Koren and Danielssen, 1875
- *Phascolion strombi* (Montague, 1804)
- *Phascolopsis gouldi* (Pourtales, 1851)
- *Sipunculus norvegicus* Koren and Danielssen, 1875

ECHIURA
- *Bonellia thomensis* (Gmelin, 1788)
- *Echiurus echiurus* (Pallas, 1774)
- *Echiurus* sp.
- *Ikedella akaeta* (Zenkevitch, 1958)
- *Maxmuelleria lankesteri* (Herdman, 1898)
- *Prometor grandis* (Zenkevitch, 1957)
- *Protobonellia* sp.
- *Sluiterina sibogae* (Sluiter, 1902)
- *Sluiterina* sp.

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Table 4 (continued)

- MOLLUSCA
  - Polyplacophora
  - Gastropoda
    - Prosobranchia
      - Archaeogastropoda
        - Fissurelidae
          - *Puncturella noachina* (Linnaeus, 1771)
        - Lepetidae
          - *Lepeta caeca* (Müller, 1776)
        - Trochidae
          - *Calliostoma occidentalis* (Mighels and Adams, 1842)
          - *Margarites costalis* (Gould, 1841)
          - *Margarites groenlandicus* (Gmelin, 1791)
          - *Margarites helicinus* (Phipps, 1774)
          - *Margarites* sp.
          - *Solariella lamellosa* Verrill and Smith, 1880
          - *Solariella obscura* (Couthouy, 1838)
          - *Solariella* sp.
      - Mesogastropoda
        - Littorinidae
          - *Littorina obtusata* (Linnaeus, 1758)
        - Rissoidae
          - *Alvania brychia* (Verrill, 1884)
          - *Alvania pelagica* (Stimpson, 1851)
          - *Alvania areolata* Stimpson, 1851
          - *Alvania* sp.
        - Turritellidae
          - *Tachyrhynchus erosus* (Couthouy, 1838)
          - *Turritellopsis acicula* (Stimpson, 1851)
        - Cerithiidae
          - *Cerithiella* sp.
          - *Diastoma alternatus* (Say, 1822)
        - Epitoniidae
          - *Epitonium dallianum* Verrill and Smith, 1880
          - *Epitonium greenlandicum* (Perry, 1811)
        - Melanellidae
          - *Couthouyella striatula* (Couthouy, 1839)
        - Aclididae
          - *Aclis verrilli* Bartsch, 1911
        - Trichotropidae
          - *Trichotropis borealis* Broderip and Sowerby, 1829
        - Crepidulidae
          - *Crepidula fornicata* Linnaeus, 1767
          - *Crepidula plana* Say, 1822
          - *Crucibulum striatum* Say, 1824
        - Aporrhaidae
          - *Aporrhais occidentalis* Beck, 1836
        - Velutinidae
          - *Velutina velutina* (Müller, 1776)
          - *Velutina undata* (Brown, 1839)
          - *Velutina* sp.
        - Naticidae
          - *Lunatia heros* (Say, 1822)
          - *Lunatia triseriata* (Say, 1826)
          - *Lunatia pallida* (Broderip, and Sowerby, 1829)
          - *Lunatia* sp.
          - *Natica clausa* Broderip and Sowerby, 1829
          - *Natica pusilla* Say, 1822
          - *Polinices duplicatus* (Say, 1822)
          - *Polinices immaculatus* (Totten, 1835)
          - *Polinices* sp.
      - Neogastropoda
        - Muricidae
          - *Boreotrophon clathratus* (Linnaeus, 1758)
          - *Eupleura caudata* (Say, 1822)
        - Columbellidae
          - *Amphissa haliaeeti* (Jeffreys, 1867)
          - *Anachis lafresnayi* (Fischer and Bernardi, 1856)
          - *Anachis* sp.
          - *Mitrella lunata* (Say, 1826)
          - *Mitrella pura* (Verrill, 1882)
          - *Mitrella rosacea* (Gould, 1841)
          - *Mitrella* sp.
        - Buccinidae
          - *Buccinum undatum* Linnaeus, 1758
          - *Buccinum* sp.
          - *Colus caelatus* (Verrill and Smith, 1880)
          - *Colus obesus* (Verrill, 1884)
          - *Colus parvus* (Verrill and Smith, 1882)
          - *Colus pygmaeus* (Gould, 1841)
          - *Colus* sp.
          - *Neptunea decemcostata* (Say, 1826)
          - *Neptunea despecta* (Linnaeus, 1758)
          - *Neptunea* sp.
        - Melongenidae
          - *Busycon canaliculatus* (Linnaeus, 1758)
        - Nassariidae
          - *Ilyanassa obsoleta* (Say, 1822)
          - *Nassarius trivittatus* (Say, 1822)
          - *Nassarius vibex* (Say, 1822)
        - Cancellariidae
          - *Admete couthouyi* (Jay, 1839)
        - Turridae
          - *Oenopota decussata* (Couthouy, 1839)
          - *Oenopota harpularia* (Couthouy, 1838)
          - *Oenopota incisula* (Verrill, 1882)
          - *Pleurotomella agassizi agassizi* Verrill and Smith, 1880
          - *Pleurotomella blakeana* (Dall, 1889)
          - *Pleurotemella curta curta* (Verrill, 1884)
          - *Pleurotomella packardi packardi* (Verrill, 1872)
          - *Propebela elegans* (Möller, 1842)
          - *Propebela exarata* (Möller, 1842)
          - *Propebela turricula* (Montagu, 1803)
        - Pyramidellidae
          - *Odostomia dealbata* (Stimpson, 1851)
          - *Odostomia dux* Dall and Bartsch, 1906
          - *Odostomia* sp.
          - *Turbonilla bushiana* Verrill, 1882
          - *Turbonilla elegantula* Verrill, 1882
          - *Turbonilla nivea* (Stimpson, 1851)
          - *Turbonilla polita* (Verrill, 1872)
          - *Turbonilla* sp.
      - Opisthobranchia
        - Acteonidae
          - *Acteon* sp.
        - Ringiculidae
          - *Ringicula nitida* Verrill, 1873
        - Actiocinidae
          - *Acteocina canaliculata* (Say, 1822)
          - *Retusa obtusa* (Montagu, 1807)

continued on next page

Table 4 (continued)

- Scaphandridae
  - *Cylichna alba* (Brown, 1827)
  - *Cylichna gouldi* (Couthouy, 1839)
  - *Cylichna vortex* (Dall, 1881)
  - *Cylichna* sp.
  - *Scaphander punctostriatus* Mighels, 1841
- Philinidae
  - *Philine lima* (Brown, 1827)
  - *Philine quadrata* (S. Wood, 1839)
  - *Philine* sp.
- Akeridae
  - *Haminoea* sp.
- Pleurobranchidae
  - *Pleurobranchaea* sp.

Nudibranchia
- Dendronotidae
  - *Dendronotus frondosus* (Ascanius, 1774)

Bivalvia

Palaeotoxodonta

Nuculoida
- Nuculidae
  - *Nucula delphinodonta* Mighels and Adams, 1842
  - *Nucula proxima* Say, 1822
  - *Nucula tenuis* Montagu, 1808
  - *Nucula* sp.
- Malletiidae
  - *Malletia obtusa* G.O. Sars, 1872
  - *Saturnia subovata* Verrill, and Bush, 1897
- Nuculanidae
  - *Nuculana acuta* (Conrad, 1831)
  - *Nuculana pernula* (Müller, 1771)
  - *Nuculana tenuisulcata* (Couthouy, 1838)
  - *Nuculana* sp.
  - *Portlandia fraterna* (Verrill and Bush, 1898)
  - *Portlandia frigida* (Torrell, 1859)
  - *Portlandia inconspicua* (Verrill and Bush 1898)
  - *Portlandia inflata* (Verrill, and Bush, 1897)
  - *Portlandia iris* (Verrill and Bush, 1897)
  - *Portlandia lenticula* (Möller, 1842)
  - *Portlandia lucida* (Loven, 1846)
  - *Yoldia limatula* (Say, 1831)
  - *Yoldia myalis* (Couthouy, 1838)
  - *Yoldia regularis* Verrill, 1884
  - *Yoldia sapotilla* (Gould,1841)
  - *Yoldia thraciaeformis* Storer, 1838
  - *Yoldia* sp.

Cryptodonta

Solemyoida
- Solemyacidae
  - *Solemya velum* Say, 1822

Pteriomorphia

Arcoida
- Arcidae
  - *Anadara ovalis* (Bruguière, 1789)
  - *Anadara transversa* (Say, 1822)
  - *Bathyarca anomala* (Verrill and Bush, 1898)
  - *Bathyarca pectunculoides* (Scacchi, 1833)
  - *Bathyarca* sp.
- Limopsidae
  - *Limopsis affinis* Verrill, 1885
  - *Limopsis cristata* Jeffreys, 1876
  - *Limopsis minuta* Philippi, 1836
  - *Limopsis sulcata* Verrill and Bush, 1898
  - *Limopsis* sp.

Mytiloida
- Mytilidae
  - *Crenella decussata* (Montagu, 1808)
  - *Crenella glandula* (Totten, 1834)
  - *Crenella* sp.
  - *Dacrydium vitreum* (Holböll in Möller, 1842)
  - *Modiolus modiolus* (Linnaeus, 1758)
  - *Musculus corrugatus* (Stimpson, 1851)
  - *Musculus discors* (Linnaeus, 1767)
  - *Musculus niger* (Gray, 1824)
  - *Musculus* sp.
  - *Mytilus edulis* Linnaeus, 1758
  - *Mytilus* sp.

Pterioida
- Pectinidae
  - *Chlamys islandica* (Müller, 1776)
  - *Cyclopecten pustulosus* Verrill, 1873
  - *Placopecten magellanicus* (Gmelin, 1791)
- Anomiidae
  - *Anommia simplex* Orbigny, 1842
  - *Anomia squamula* Linnaeus, 1758
  - *Anomia* sp.
- Limidae
  - *Limatula subauriculata* (Montagu, 1808)
  - *Limatula* sp.

Heterodonta

Veneroida
- Lucinidae
  - *Lucinoma blakeana* Bush, 1883
  - *Lucinoma filosa* (Stimpson, 1851)
  - *Lucinoma* sp.
- Thyasiridae
  - *Thyasira equalis* Verrill and Bush, 1898
  - *Thyasira ferruginea* Winckworth, 1932
  - *Thyasira flexuosa* (Montagu, 1803)
  - *Thyasira flexuosa* forma *gouldii* Philippi, 1845
  - *Thyasira pygmaea* Verrill and Bush, 1898
  - *Thyasira subovata* Jeffreys, 1881
  - *Thyasira trisinuata* Orbigny, 1842
  - *Thyasira* sp.
- Lasaeidae
  - *Aligena elevata* (Stimpson, 1851)
- Leptonidae
  - *Montacuta* sp.
- Carditidae
  - *Cyclocardia borealis* Conrad, 1831
  - *Cyclocardia* sp.
- Astartidae
  - *Astarte borealis* (Schumacher, 1817)
  - *Astarte castanea* (Say, 1822)
  - *Astarte crenata subequilatera* Sowerby, 1854
  - *Astarte elliptica* (Brown, 1827)
  - *Astarte montagui* (Dillwyn, 1817)
  - *Astarte nana* Dall, 1886
  - *Astarte quadrans* Gould, 1841
  - *Astarte smithii* Gould, 1841
  - *Astarte undata* Gould, 1841
  - *Astarte* sp.

continued on next page

Table 4 (continued)

- Cardiidae
  - *Cerastoderma pinnulatum* (Conrad, 1831)
  - *Laevicardium mortoni* (Conrad, 1830)
- Mactridae
  - *Mulinia lateralis* (Say, 1822)
  - *Spisula solidissima* (Dillwyn, 1817)
- Mesodesmatidae
  - *Mesodesma* sp.
- Solenidae
  - *Ensis directus* Conrad, 1843
  - *Siliqua costata* Say, 1822
- Tellinidae
  - *Macoma calcarea* (Gmelin, 1791)
  - *Macoma* sp.
  - *Tellina agilis* Stimpson, 1858
  - *Tellina* sp.
- Arcticidae
  - *Arctica islandica* (Linnaeus, 1767)
- Veneridae
  - *Gemma gemma* (Totten, 1834)
  - *Mercenaria mercenaria* (Linnaeus, 1758)
  - *Pitar morrhuanus* Linsley, 1845

- Myoida
  - Myidae
    - *Mya arenaria* Linnaeus, 1758
  - Corbulidae
    - *Corbula contracta* C.B. Adams, 1852
    - *Corbula* sp.
  - Hiatellidae
    - *Cyrtodaria siliqua* (Spengler, 1793)
    - *Hiatella arctica* (Linnaeus, 1767)
    - *Hiatella striata* (Fleuriau, 1802)
    - *Hiatella* sp.
    - *Panomya arctica* (Lamarck, 1818)
    - *Panomya* sp.

- Anomalodesmata
  - Pholadomyoida
    - Pandoridae
      - *Pandora gouldiana* Dall, 1886
      - *Pandora inflata* Boss and Merrill, 1965
      - *Pandora inornata* Verrill and Bush, 1898
      - *Pandora* sp.
    - Lyonsiidae
      - *Lyonsia arenosa* Möller, 1842
      - *Lyonsia hyalina* Conrad, 1830
      - *Lyonsia* sp.
    - Periplomatidae
      - *Periploma fragile* (Totten, 1835)
      - *Periploma leanum* (Conrad, 1830)
      - *Periploma papyratium* (Say, 1822)
      - *Periploma* sp.
    - Thraciidae
      - *Thracia myopsis* Möller, 1842
      - *Thracia* sp.
    - Cuspidariidae
      - *Cardiomya perrostrata* (Dall, 1881)
      - *Cuspidaria glacialis* (G.O. Sars, 1878)
      - *Cuspidaria obesa* (Lovén, 1846)
      - *Cuspidaria parva* Verrill and Bush, 1898
      - *Cuspidaria pellucida* Stimpson, 1853
      - *Cuspidaria* sp.

- Scaphopoda
  - Dentaliidae
    - *Bathoxiphus ensiculus* (Jeffreys, 1877)
    - *Cadulus agassizii* Dall, 1881
    - *Cadulus cylindratus* Jeffreys, 1877
    - *Cadulus pandionis* Verrill and Smith, 1880
    - *Cadulus rushii* Pilsbry and Sharp, 1898
    - *Cadulus* sp.
    - *Dentalium entale stimpsoni* Henderson, 1920
    - *Dentalium meridionale* Pilsbry and Sharp, 1897
    - *Dentalium occidentale* Stimpson, 1851
    - *Dentalium* sp.
- Cephalopoda
  - *Octopus* sp.
  - *Rossia* sp.

- ARTHROPODA
  - Pycnogonida
    - *Achelia scabra* Wilson, 1880
    - *Achelia spinosa* (Stimpson, 1853)
    - *Anoplodactylus lentus* Wilson, 1878
    - *Nymphon brevitarse* Krøyer, 1844
    - *Nymphon grossipes* (O. Fabricius?) Krøyer, 1780
    - *Nymphon hirtipes* Bell, 1853
    - *Nymphon macrum* Wilson, 1880
    - *Nymphon stroemi* Krøyer, 1844
    - *Paranymphon spinosum* Caullery, 1896
    - *Pycnogonium littorale* (Strom, 1762)
  - Crustacea
    - Cirripedia
      - *Balanus* sp.
      - *Lepas* sp.
    - Copepoda
      - *Calanus* sp.
      - *Caligus* sp.
    - Cumacea
      - *Brachydiastylis resima* (Krøyer, 1846)
      - *Campylaspis affinis* Sars, 1870
      - *Campylaspis rubicunda* (Lilljeborg, 1855)
      - *Cyclaspis longicaudata* G.O. Sars, 1864
      - *Diastylis cornuifer* (Blake, 1929)
      - *Diastylis polita* S.I. Smith, 1879
      - *Diastylis quadrispinosa* G.O. Sars, 1871
      - *Diastylis rathkei* (Krøyer, 1841)
      - *Diastylis sculpta* G.O. Sars, 1871
      - *Diastylis* sp.
      - *Eudorella emarginata* (Krøyer, 1846)
      - *Eudorella hispida* Sars, 1871
      - *Eudorella truncatula* (Bate, 1855)
      - *Eudorella* sp.
      - *Eudorellopsis deformis* (Krøyer, 1846)
      - *Eudorellopsis* sp.
      - *Hemilamprops cristata* (Sars, 1870)
      - *Lamprops quadriplicata* S.I. Smith, 1879
      - *Lamprops fuscata* Sars, 1865
      - *Lamprops* sp.
      - *Leptostylis longimana* (Sars, 1865)
      - *Leptostylis macrura* G.O. Sars, 1869
      - *Leptostylis* sp.
      - *Leucon americanus* Zimmer, 1943
      - *Leucon nasicoides* Lilljeborg, 1855
      - *Oxyrostylis smithi* Calman, 1912

continued on next page

Table 4 (continued)

Cumacea, continued
Petalosarsia declivis (G.O. Sars, 1865)
Pseudoleptocuma minor (Calman, 1912)
Isopoda
Calathura branchiata (Stimpson, 1853)
Calathura sp.
Chiridotea arenicola Wigley, 1960
Chiridotea tuftsi (Stimpson, 1883)
Chiridotea sp.
Cirolana concharum (Stimpson, 1853)
Cirolana impressa (Harger, 1818)
Cirolana polita (Stimpson, 1853)
Cirolana sp.
Cyathura polita (Stimpson, 1855)
Cyathura sp.
Edotea acuta (Richardson, 1905)
Edotea triloba (Say, 1818)
Erichsonella filiformis (Say, 1818)
Idotea phosphorea (Harger, 1873)
Janira alta (Stimpson, 1853)
Pseudarachna sp.
Ptilanthura tenuis (Harger, 1879)
Ptilanthura sp.
Amphipoda
Caprellidea
Caprellidae
Aeginina longicornis (Krøyer, 1842-43)
Aeginina sp.
Caprella linearis (Linnaeus, 1767)
Caprella penantis Leach, 1814
Caprella septentrionalis Krøyer, 1838
Caprella unica Mayer, 1903
Caprella sp.
Luconacia incerta Mayer, 1903
Mayerella limicola Huntsman, 1915
Proaeginina norvegica (Stephensen, 1931)
Hyperiidea
Hyperiidae
Hyperia sp.
Parathemisto gaudichaudii (Milne-Edwards, 1840)
Parathemisto sp.
Phronima sedentaria (Forskal, 1775)
Vibilia sp.
Gammaridea
Acanthonotozomatidae
Acanthonotozoma serratum (Fabricius, 1780)
Ampeliscidae
Ampelisca abdita Mills, 1964
Ampelisca agassizi (Judd, 1896)
Ampelisca declivitatus Mills, 1967
Ampelisca eschrichti Krøyer, 1842
Ampelisca macrocephala Lilljeborg, 1852
Ampelisca vadorum Mills, 1963
Ampelisca verrilli Mills, 1967
Ampelisca sp.
Byblis gaimardi (Krøyer, 1846)
Byblis serrata (Smith, 1873)
Byblis sp.
Haploops tubicola Lilljeborg, 1856
Haploops sp.
Amphilochidae
Amphilochoides odontyx (Boeck, 1871)
Gitanopsis arctica G.O. Sars, 1895
Amphithoidae
Amphithoe rubricata (Montagu, 1808)
Aoridae
Lembos smithi Holmes, 1905
Lembos sp.
Leptocheirus pinguis (Stimpson, 1853)
Leptocheirus sp.
Microdeutopis gryllotalpa Costa, 1853
Pseudunciola obliqua (Shoemaker, 1949)
Unciola dissimilis Shoemaker, 1945
Unciola inermis Shoemaker, 1945
Unciola irrorata Say, 1818
Unciola leucopis (Krøyer, 1845)
Unciola serrata Shoemaker, 1945
Unciola spicata Shoemaker, 1945
Unciola sp.
Argissidae
Argissa hamatipes (Norman, 1869)
Bateidae
Batea catharinensis Müller, 1865
Calliopiidae
Calliopius laeviusculus (Krøyer, 1838)
Halirages fulvocinctus (M. Sars, 1854)
Haliragoides inermis (G.O. Sars, 1882)
Hippomedon serratus Holmes, 1905
Corophiidae
Corophium crassicorne Bruzelius, 1859
Corophium insidiosum Crawford, 1937
Corophium volutator (Pallas, 1766)
Corophium sp.
Siphonocetes smithianus Rathbun, 1908
Siphonocetes sp.
Eusiridae
Eusirus cuspidatus Krøyer, 1845
Rhachotropis distincta (Holmes, 1908)
Rhachotropis inflata (G.O. Sars, 1882)
Rhachotropis oculata (Hansen, 1887)
Gammarus annulatus Smith, 1873
Gammarus pallustris Bousfield, 1969
Gammarus sp.
Haustoriidae
Acanthohaustorius intermedius Bousfield, 1965
Acanthohaustorius millsi Bousfield, 1965
Acanthohaustorius similis Frame, 1980
Acanthohaustorius spinosus Bousfield, 1962
Haustorius arenarius (Slabber, 1769)
Haustorius sp.
Parahaustorius attenuatus Bousfield, 1965
Parahaustorius holmesi Bousfield, 1965
Parahaustorius longimerus Bousfield, 1965
Protohaustorius deichmannae Bousfield, 1965
Protohaustorius wigleyi Bousfield, 1965
Pseudohaustorius borealis Bousfield, 1965
Ischyroceridae
Ericthonius brasiliensis (Dana, 1853)
Ericthonius rubricornis Smith, 1873
Ericthonius sp.
Ischyroceros anguipes Krøyer, 1838

continued on next page

Table 4 (continued)

- Ischyroceridae, continued
  - *Ischyroceros megacheir* (Boeck, 1871)
  - *Ischyroceros* sp.
- Lysianassidae
  - *Anonyx debruynii* Hoek, 1882
  - *Anonyx lilljeborgi* Boeck, 1871
  - *Anonyx nugax* (Phipps, 1774)
  - *Anonyx sarsi* Steele and Brunel, 1968
  - *Anonyx* sp.
  - *Hippomedon propinguus* Sars, 1895
  - *Hippomedon serratus* Holmes, 1905
  - *Hippomedon* sp.
  - *Lysianopsis alba* Holmes, 1905
  - *Orchomene groenlandica* (Hansen, 1887)
  - *Orchomene minuta* Krøyer, 1846
  - *Orchomene pinguis* Boeck, 1861
  - *Orchomene* sp.
  - *Psammonyx nobilis* Stimpson, 1853
  - *Tmetonyx cicada* O. Fabricius, 1780
  - *Tmetonyx* sp.
  - *Tryphosella nanoides* Lilljeborg, 1865
- Melitidae
  - *Casco bigelowi* (Blake, 1929)
  - *Eriopisa elongata* (Bruzelius, 1859)
  - *Maera danae* Stimpson, 1853
  - *Maera loveni* (Bruzelius, 1859)
  - *Maera* sp.
  - *Melita dentata* Krøyer, 1842
  - *Melita palmata* (Montagu, 1894)
  - *Melita* sp.
- Melphidippidae
  - *Melphidippa goesi* Stebbing, 1899
  - *Melphidippa* sp.
- Oedicerotidae
  - *Bathymedon sausserei* (Boeck, 1871)
  - *Monoculodes edwardsi* Holmes, 1908
  - *Monoculodes intermedius* Shoemaker, 1930
  - *Monoculodes latimanus* (Goes, 1866)
  - *Monoculodes longicornis* (Boeck, 1871)
  - *Paroediceros* sp.
  - *Synchelidium americanum* Bousfield, 1973
  - *Westwoodilla megalops* (G.O. Sars, 1882) .
- Paramphithoidae
  - *Epimeria loricata* G.O. Sars, 1879
- Pardaliscidae
  - *Halice abyssi* Boeck, 1871
  - *Pardalisca cuspidata* Krøyer, 1842
- Photidae
  - *Gammaropsis maculatus* (Johnson, 1827)
  - *Photis dentata* Shoemaker, 1945
  - *Photis macrocoxa* Shoemaker, 1945
  - *Photis reinhardi* Krøyer, 1842
  - *Photis* sp.
  - *Podoceropsis nitida* (Stimpson, 1853)
  - *Protomedia fasciata* Krøyer, 1842
- Pleustidae
  - *Neopleustes pulchellus* Krøyer, 1846
  - *Parapleustes* sp.
  - *Pleustes panoplus* Krøyer, 1838
  - *Pleustes glaber* Boeck, 1861
  - *Stenopleustes gracilis* Holmes, 1905
  - *Stenopleustes inermis* Shoemaker, 1949
  - *Stenopleustes latipes* (M. Sars, 1895)
- Podoceridae
  - *Dyopedus articus* (Murdoch, 1884)
  - *Dyopedus monacantha* (Metzger, 1875)
  - *Dulichia porrecta* (Bate, 1857)
  - *Dulichia tuberculata* Boeck, 1870
  - *Dulichia* sp.
  - *Paradulichia typica* Boeck, 1870
  - *Paradulichia* sp.
- Pontogeneidae
  - *Pontogeneia inermis* (Krøyer, 1842)
  - *Pontogeneia* sp.
- Pontoporeiidae
  - *Amphiporea gigantea* Bousfield, 1973
  - *Amphiporea lawrenciana* Shoemaker, 1929
  - *Amphiporea virginiana* Shoemaker, 1933
  - *Bathyporeia quoddyensis* Shoemaker, 1949
- Stegocephalidae
  - *Anadaniopsis nordlandica* (Boeck, 1871)
  - *Stegocephalus inflatus* Krøyer, 1842
- Stenothoidae
  - *Stenothoe minuta* Holmes, 1905
  - *Stenula peltata* (Smith, 1873)
- Synopiidae
  - *Syrrhoe crenulata* Goes, 1866
  - *Syrrhoe spiniferum* (Stimpson, 1853)
- Mysidacea
  - *Erythrops erythrophthalma* (Goes, 1864)
  - *Erythrops* sp.
  - *Mysidopsis bigelowi* Tattersall, 1926
  - *Neomysis americana* (S.I. Smith, 1873)
  - *Neomysis* sp.
- Decapoda
  - Caridea
    - *Crangon septemspinosa* Say, 1818
    - *Dichelopandalus leptocerus* (Smith, 1881)
    - *Eualus pusiolus* (Krøyer, 1841)
    - *Pandalus montagui* Leach, 1813 or 1814
    - *Pandalus propinquus* G.O. Sars, 1869
    - *Pandalus* sp.
    - *Pontophilus brevirostris* Smith, 1881
    - *Spirontocaris lilljeborgii* (Danielssen, 1859)
    - *Spirontocaris* sp.
  - Astacidea
    - *Homarus americanus* H. Milne-Edwards, 1837
  - Anomura
    - *Axius serratus* Stimpson, 1852
    - *Callianassa atlantica* Rathbun, 1926
    - *Callianassa biformis* Biffar, 1971
    - *Calocaris templemani* (Squires, 1965)
    - *Catapagurus gracilis* (Smith, 1881)
    - *Munida iris* A. Milne-Edwards, 1880
    - *Munida valida* Smith, 1883
    - *Pagurus acadianus* Benedict, 1901
    - *Pagurus annulipes* Stimpson, 1860
    - *Pagurus arcuatus* Squires, 1964
    - *Pagurus longicarpus* Say, 1817
    - *Pagurus politus* (Smith, 1882)
    - *Pagurus pollicaris* Say, 1817
    - *Pagurus pubescens* Krøyer, 1838

continued on next page

Table 4 (continued)

- Anomura, continued
  - *Upogebia affinis* (Say, 1817)
- Brachyura
  - *Cancer borealis* Stimpson, 1859
  - *Cancer irroratus* Say, 1817
  - *Euprognatha rastellifera* Stimpson, 1871
  - *Geryon quinquedens* Smith, 1897
  - *Hexapanopeus angustifrons* (Benedict and Rathbun, 1891)
  - *Hyas coarctatus* Leach, 1815
  - *Hyas* sp.
  - *Libinia dubia* H. Milne-Edwards, 1834
  - *Libinia* sp.
  - *Neopanope texana sayi* (Smith, 1869)
  - *Ocypode* sp.
  - *Pelia mutica* (Gibbes, 1850)
  - *Pinnixa chaetopterana* Stimpson, 1860
  - *Pinnixa sayana* Stimpson, 1860
  - *Pinnixa* sp.

BRYOZOA

- Ctenostomata
  - Alcyonidiidae
    - *Alcyonidium mamillatum* Alder, 1857
    - *Alcyonidium* sp.
  - Flustrellidae
    - *Flustrellidra* sp.
- Cyclostomata
  - Crisiidae
    - *Crisia cribraria* Stimpson, 1853
    - *Crisia denticulata* (Lamarck, 1816)
  - Oncousoeciidae
    - *Oncousoecia canadensis* Osburn, 1933
    - *Oncousoecia diastoporoides* (Norman, 1868)
    - *Oncousoecia* sp.
  - Tubuliporidae
    - *Idmonea atlantica* Johnston, 1847
    - *Idmonea* sp.
    - *Tubulipora liliacea* (Pallas, 1766)
    - *Tubulipora lobulata* Hassall, 1841
    - *Tubulipora* sp.
  - Diaperoeciidae
    - *Diaperoecia harmeri* Osburn, 1933
    - *Diplosolen obelium* (Johnston, 1838)
    - *Entalophora* sp.
  - Frondiporidae
    - *Defrancia* sp.
- Cheilostomata
  - Alderinidae
    - *Amphiblestrum flemingii* (Busk, 1854)
    - *Amphiblestrum trifolium* (Searles Wood, 1850)
    - *Cauloramphus cymbaeformis* (Hincks, 1887)
  - Bugulidae
    - *Bugula elongata* Nordgaard, 1906
    - *Bugula turrita* (Desor, 1848)
    - *Bugula* sp.
    - *Dendrobeania murrayana* (Johnston, 1847)
    - *Dendrobeania* sp.
  - Calloporidae
    - *Callopora aurita* (Hincks, 1877)
    - *Callopora craticula* (Alder, 1857)
    - *Callopora lineata* (Linnaeus, 1767)
    - *Callopora whiteavesi* Norman, 1903
    - *Callopora* sp.
  - Cellariidae
    - *Cellaria* sp.
  - Celliporidae
    - *Cellepora canaliculata* Busk, 1884
    - *Cellepora* sp.
  - Cheiloporinidae
    - *Cryptosula pallasiana* (Moll, 1803)
  - Cribrilinidae
    - *Cribrilina punctata* (Hassall, 1842)
    - *Cribrilina* sp.
  - Electridae
    - *Electra hastingsae* Marcus, 1938
    - *Electra pilosa* (Linnaeus, 1767)
    - *Pyripora catenularia* (Jameson, 1814)
  - Eucrateidae
    - *Eucratea loricata* (Linnaeus, 1758)
  - Hippoporinidae
    - *Hippodiplosia americana* (Verrill, 1875)
    - *Hippodiplosia pertusa* (Esper, 1794-97)
    - *Hippoponella hippopus* (Smitt, 1867)
  - Hippothoidae
    - *Hippothoa hyalina* (Linnaeus, 1767)
  - Membraniporidae
    - *Conopeum reticulum* (Linnaeus, 1767)
    - *Membranipora* sp.
  - Microporellidae
    - *Microporella ciliata* (Pallas, 1766)
  - Mucronellidae
    - *Mucronella immersa* (Fleming, 1847)
    - *Mucronella ventricosa* (Hassall, 1842)
    - *Palmicellaria skenei* (Ellis and Solander, 1786)
    - *Porella plana* (Dawson, 1859)
    - *Porella proboscidea* Hincks, 1888
    - *Porella propinqua* (Smitt, 1867)
    - *Pseudoflustra* sp.
    - *Rhamphostomella bilaminata* (Hincks, 1877)
    - *Rhamphostomella ovata* (Smitt, 1867)
    - *Rhamphostomella* sp.
    - *Smittina bella* (Busk, 1860)
    - *Smittina reduplicata* Osburn, 1933
    - *Smittina rigida* Lorenz, 1886
    - *Smittina trispinosa* (Johnston, 1838)
    - *Smittina* sp.
  - Schizoporellidae
    - *Schizomavella auriculata* (Hassall, 1842)
    - *Schizoporella biaperta* (Michelin, 1841-42)
    - *Schizoporella unicornis* (Johnston, 1847)
  - Scrupariinidae
    - *Haplota clavata* (Hincks, 1857)
  - Scrupocellariidae
    - *Caberea ellisii* (Fleming, 1828)
    - *Scrupocellaria scabra* (Fabricius, 1780)
    - *Tricellaria gracilis* (Van Beneden, 1848)
    - *Tricellaria* sp.
  - Gigantoporidae
    - *Tessaradoma gracile* (M. Sars, 1851)
  - Stomachetosellidae
    - *Escharopsis sarsi* (Smitt, 1868)
    - *Stomachetosella* sp.

continued on next page

Table 4 (continued)

BRACHIOPODA
- *Terebratulina* sp.

ECHINODERMATA
- Holothuroidea
  - Apodida
    - *Chirodota* sp.
    - *Labidoplax buskii* (McIntosh, 1866)
    - *Myritrochus* sp.
    - *Synapta* sp.
    - *Trochoderma* sp.
  - Aspidochirotida
    - *Astichopus* sp.
  - Dendrochirotida
    - *Cucumaria planci* Marenzeller, 1893
    - *Cucumaria* sp.
    - *Havelockia scabra* (Verrill, 1873)
    - *Psolus fabricii* Duben and Koren, 1846
    - *Psolus phantapus* (Strussenfeldt, 1765)
    - *Psolus valvatus* Østergren in Grieg, 1913
    - *Psolus* sp.
    - *Stereoderma unisemita* (Stimpson, 1851)
    - *Thyone fusus* (Müller, 1788)
    - *Thyone* sp.
    - *Thyonidium pellucidum* Duben and Koren, 1844
  - Molpadiida
    - *Caudina arenata* (Gould, 1841)
    - *Molpadia oolitica* (Pourtales, 1851)
    - *Molpadia* sp.
  - Dactylochirotida
    - *Echinocucumis* sp.
- Echinoidea
  - Camarodonta
    - *Strongylocentrotus droebachiensis* (Müller, 1776)
  - Clypeastroidea
    - *Echinarachnius parma* (Lamarck, 1816)
    - *Echinocyamus grandiporus* Mortensen, 1907
  - Spatangoida
    - *Aceste bellidifera* Wyville Thompson, 1877
    - *Aeropsis rostrata* Norman, 1876
    - *Brisaster fragilis* (Duben and Koren, 1844)
    - *Brissopsis atlantica* Mortensen, 1907
    - *Schizaster orbignyanus* A. Agassiz, 1883
    - *Schizaster* sp.
- Ophiuroidea
  - Amphilepididae
    - *Amphilepis ingolfiana* Mortensen, 1933
  - Amphiuridae
    - *Amphilimna olivacea* (Lyman, 1869)
    - *Amphilimna* sp.
    - *Amphioplus abditus* (Verrill, 1872)
    - *Amphioplus macilentus* (Verrill, 1882)
    - *Amphioplus* sp.
    - *Amphiura otteri* Ljungman, 1871
    - *Amphiura fragilis* (Verrill, 1885)
    - *Amphiura grandisquama* Lyman, 1869
    - *Amphiura* sp.
    - *Axiognathus squamatus* (delle Chiaje, 1828)
    - *Axiognathus* sp.
  - Ophiacanthidae
    - *Ophiacantha abyssicola* (E. Forbes, 1843)
    - *Ophiacantha bidentata* (Retzius, 1805)
    - *Ophiacantha* sp.
    - *Ophiochiton tenuispinus* (Verrill, 1884)
    - *Ophiocten scutatum* Koehler, 1896
    - *Ophiocten sericeum* (Forbes, 1852)
    - *Ophiomusium lymani* Thompson, 1873
    - *Ophiura ljungmani* (Lyman, 1878)
    - *Ophiura robusta* (Ayres, 1852)
    - *Ophiura sarsi* Lütken, 1858
    - *Ophiura* sp.
- Asteroidea
  - Asteriidae
    - *Asterias forbesi* (Desor, 1848)
    - *Asterias vulgaris* (Verrill, 1866)
    - *Asterias* sp.
    - *Leptasterias* sp.
  - Astropectinidae
    - *Astropecten americana* (Verrill, 1880)
    - *Astropecten* sp.
  - Goniopectinidae
    - *Ctenodiscus crispatus* (Retzius, 1805)
    - *Ctenodiscus* sp.
  - Echinasteridae
    - *Henricia sanguinolenta* (Sars, 1844)
    - *Henricia* sp.
  - Solasteridae
    - *Solaster* sp.

HEMICHORDATA
- Enteropneusta
  - *Balanoglossus* sp.

CHORDATA
- Ascidiacea
  - *Amaroucium* sp.
  - *Bostrichobranchus* sp.
  - *Molgula* sp.

Total Macrobenthos — All Taxonomic Groups Combined

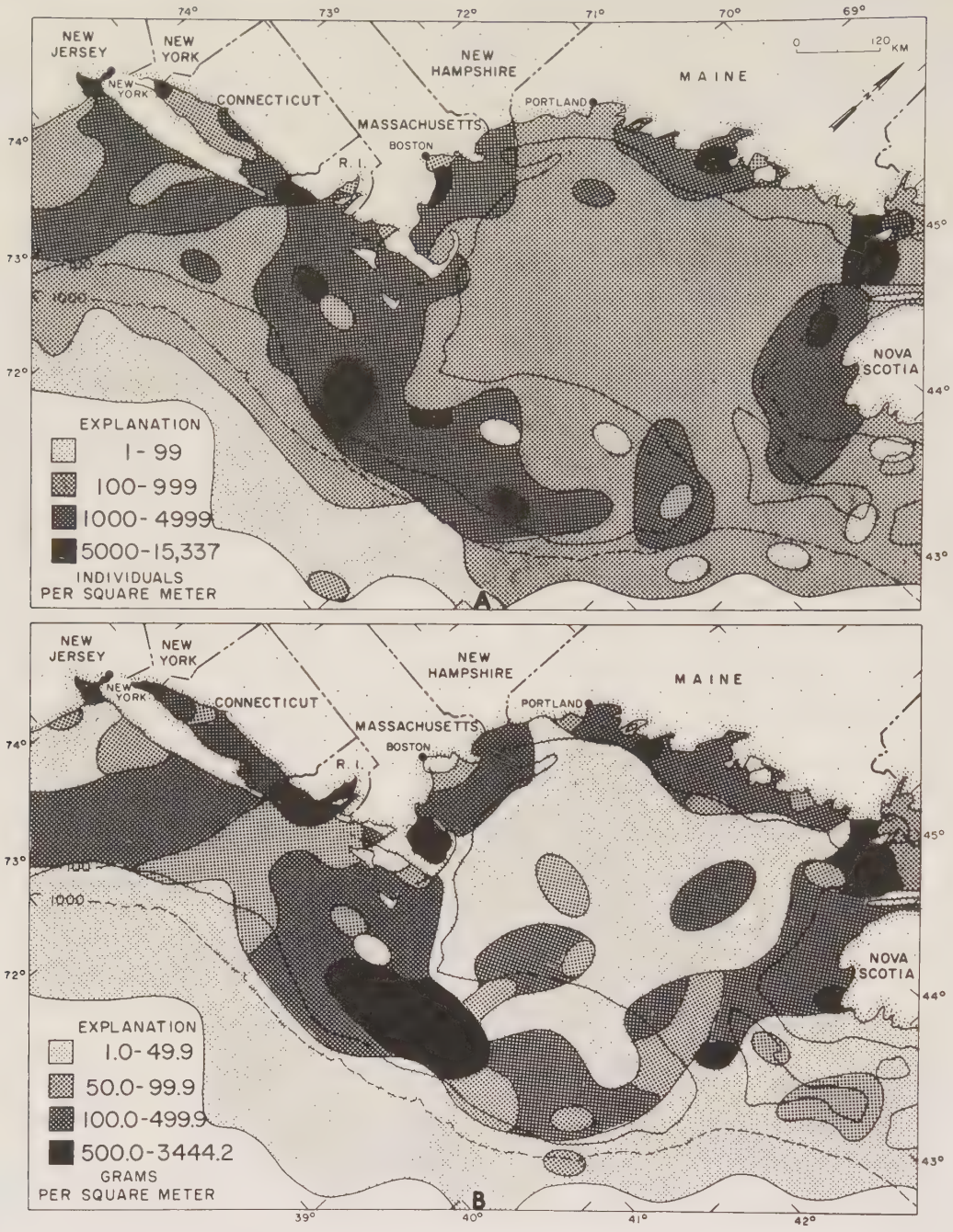
Geographic Distribution

Macrobenthic invertebrates showed clear geographic trends in abundance (Fig. 12). Both density and biomass of organisms exhibited similar patterns. Density was generally highest (1,000 to 15,000/m^2) in the coastal regions of the Gulf of Maine, on Georges Bank, and on most of the continental shelf region off Southern New England. Density was generally low (less than 100 individuals/m^2) over most of the continental rise, and moderately low (100 to 1,000/m^2) in the central Gulf of Maine, on the southeastern Scotian Shelf area, and along the continental slope. The distribution of biomass was similar to that for density. High biomass (100 to 3,400 g/m^2) was distributed around the periphery of the Gulf of Maine, on Georges Bank, on most of the continental shelf off Southern New England, and in

Table 5

Mean number and weight per square meter, total number and weight, number of samples, and percent frequency of occurrence of each taxonomic group, based on 1,076 samples.

Taxon	Mean		Total		Number of samples	Frequency of occurrence %
	No./m²	Wt./m²	No.	Wt.		
PORIFERA	1.5	2.24	1,566	2,415.82	71	6.6
COELENTERATA	32.1	7.33	34,513	7,884.63	449	41.7
Hydrozoa	6.4	0.52	6,878	560.32	126	11.7
Anthozoa	25.7	6.81	27,635	7,324.31	323	30.0
Alcyonaria	0.8	0.20	902	219.89	63	5.9
Zoantharia	22.6	6.39	24,322	6,871.85	265	24.6
Unidentified	2.2	0.22	2,411	232.57	100	9.3
PLATYHELMINTHES	0.4	0.01	381	6.44	16	1.5
Turbellaria	0.4	0.01	381	6.44	16	1.5
NEMERTEA	8.2	0.71	8,806	765.70	405	37.6
ASCHELMINTHES	2.8	0.01	3,047	8.19	98	9.1
Nematoda	2.8	0.01	3,047	8.19	98	9.1
ANNELIDA	425.0	17.41	457,283	18,727.37	1,034	96.1
POGONOPHORA	0.6	<0.01	618	3.22	56	5.2
SIPUNCULIDA	5.9	0.75	6,358	802.87	249	23.1
ECHIURA	0.1	0.30	105	327.78	17	1.6
PRIAPULIDA	<0.1	<0.01	10	4.60	4	0.4
MOLLUSCA	188.0	83.64	202,250	89,998.88	946	87.9
Polyplacophora	1.5	0.14	1,608	148.66	84	7.8
Gastropoda	17.8	2.23	19,165	2,396.85	470	43.7
Bivalvia	163.1	80.95	175,535	87,105.74	893	83.0
Scaphopoda	5.1	0.32	5,458	339.69	218	20.3
Cephalopoda	0.4	0.01	376	7.34	5	0.5
Unidentified	0.1	<0.01	108	0.60	2	0.2
ARTHROPODA	726.2	9.41	781,348	10,125.53	936	87.0
Pycnogonida	0.3	0.01	369	8.45	25	2.3
Arachnida	<0.1	<0.01	3	0.03	1	0.1
Crustacea	725.8	9.40	780,976	10,117.05	910	84.6
Ostracoda	<0.1	<0.01	19	0.19	5	0.5
Cirripedia	21.8	3.39	23,511	3,648.00	41	3.8
Copepoda	<0.1	<0.01	26	0.18	4	0.4
Cumacea	25.8	0.11	27,758	120.97	390	36.3
Tanaidacea	<0.1	<0.01	50	0.66	15	1.4
Isopoda	12.1	0.29	12,966	1,313,24	390	36.3
Amphipoda	655.8	4.16	705,612	4,478.71	862	80.1
Mysidacea	2.5	0.01	2,642	12.33	41	3.8
Decapoda	7.5	1.43	8,039	1,540.72	246	22.9
Unidentified	0.3	<0.01	353	2.07	18	1.7
BRYOZOA	15.7	1.29	16,915	1,391.00	119	11.1
BRACHIOPODA	4.5	0.89	4,793	955.31	54	5.0
ECHINODERMATA	79.3	55.00	85,331	59,182.14	772	71.8
Crinoidea	<0.1	<0.01	13	0.18	2	0.2
Holothuroidea	4.3	12.87	4,633	13,849.69	202	18.8
Echinoidea	29.3	36.75	31,512	39,540.94	293	27.2
Ophiuroidea	44.2	3.26	47,565	3,504.18	487	45.3
Asteroidea	1.5	2.13	1,608	2,287.15	144	13.4
HEMICHORDATA	0.1	0.02	101	18.67	4	0.4
CHORDATA	16.3	4.10	17,520	4,415.19	181	16.8
Ascidiacea	16.3	4.10	17,520	4,415.19	181	16.8
UNIDENTIFIED	5.8	0.27	6,199	294.42	261	24.3
Total	1,512.2	183.39	1,627,144	197,327.78		



ALL TAXA COMBINED

Figure 12

Geographic distribution of the density (A) and biomass (B) of all taxonomic groups combined. Density is expressed as number of individuals per square meter of bottom area; biomass is expressed as wet (damp) weight per square meter of bottom area.

coastal areas south of New York. Low biomass (less than 50 g/m^2) was prevalent in the central Gulf of Maine, on the southeastern Scotian Shelf, and along the continental slope and continental rise.

A few areas were characterized by a very high density (5,000/m^2 or greater) and an unusually high biomass (500 g/m^2 or more). One of these exceedingly rich areas was located at the mouth of the Bay of Fundy;

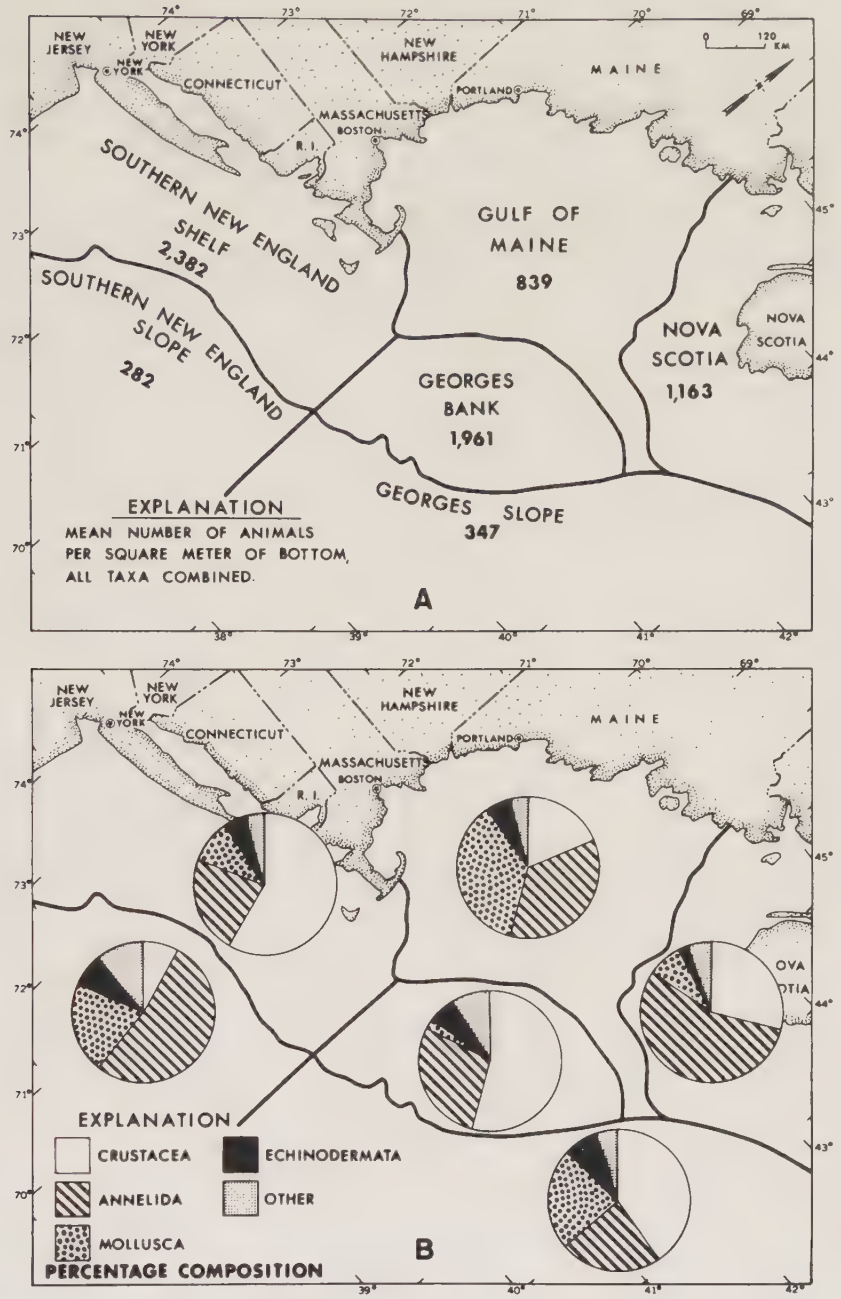


Figure 13

Quantitative composition of the total macrobenthic invertebrate fauna in relation to the six standard geographic subareas. A.—Mean number of individuals per square meter of bottom area; B.—Percentage composition, by density, of the major taxonomic groups.

another was located in the vicinity of the southern end of Great South Channel and southwestern Georges Bank. Several smaller rich areas were encountered in the coastal region of Rhode Island and New York. Generally, they occurred around the periphery of the Gulf of Maine and off southern New England.

Substantial differences in both biomass and density existed among the six geographic areas (Tables 6, 7; Fig. 13A). Average density was highest (2,382 and 1,961/m^2) on the Southern New England Shelf and on Georges Bank, intermediate in Nova Scotia and the Gulf of Maine, and lowest (about 300/m^2) on Georges Slope.

Table 6
Mean number of specimens of each taxon per square meter in relation to geographic area.

Taxon	Geographic areas						
	Nova Scotia	Gulf of Maine	Georges Bank	Southern New England Shelf	Georges Slope	Southern New England Slope	All areas
PORIFERA	4.8	2.7	0.6	0.5	0.3	0.2	1.5
COELENTERATA	22.2	9.2	99.7	22.6	6.7	8.5	32.1
Hydrozoa	11.5	3.3	6.8	9.9	0.1	0.8	6.4
Anthozoa	10.7	5.9	92.9	12.7	6.6	7.7	25.7
Alcyonaria	0.7	0.9	—	1.2	1.0	1.5	0.8
Zoantharia	8.2	3.6	92.5	7.3	3.0	4.3	22.6
Unidentified	1.8	1.4	0.4	4.2	2.6	1.9	2.2
PLATYHELMINTHES	0.2	<0.1	0.2	0.9	0.4	—	0.4
Turbellaria	0.2	<0.1	0.2	0.9	0.4	—	0.4
NEMERTEA	3.0	4.1	22.7	6.8	1.2	1.6	8.2
ASCHELMINTHES	0.9	3.1	1.7	4.0	2.3	2.3	2.8
Nematoda	0.9	3.1	1.7	4.0	2.3	2.3	2.8
ANNELIDA	648.4	291.3	545.6	530.8	79.9	148.6	425.0
POGONOPHORA	0.3	<0.1	—	—	3.1	5.3	0.6
SIPUNCULIDA	9.3	4.6	4.4	7.2	1.2	8.7	5.9
ECHIURA	—	0.1	—	0.1	0.4	0.2	0.1
PRIAPULIDA	—	—	—	—	0.1	0.1	<0.1
MOLLUSCA	77.2	306.2	46.8	244.2	83.1	57.9	188.0
Polyplacophora	1.9	3.6	0.1	0.9	0.6	0.2	1.5
Gastropoda	15.0	15.2	11.2	28.8	8.4	6.9	17.8
Bivalvia	50.6	276.0	34.4	212.3	69.5	45.8	163.1
Scaphopoda	9.6	11.4	1.2	1.0	4.5	4.8	5.1
Cephalopoda	<0.1	—	<0.1	1.0	0.1	0.1	0.4
Unidentified	—	—	—	0.3	<0.1	—	0.1
ARTHROPODA	329.8	150.4	1,052.4	1,386.0	137.6	21.5	726.2
Pycnogonida	0.8	0.1	0.3	0.6	0.1	—	0.3
Arachnida	—	—	<0.1	—	—	—	<0.1
Crustacea	329.0	150.3	1,052.1	1,385.4	137.5	21.5	725.9
Ostracoda	0.1	<0.1	—	—	<0.1	<0.1	<0.1
Cirripedia	35.7	6.4	2.7	52.2	—	—	21.8
Copepoda	—	—	—	<0.1	—	0.2	<0.1
Cumacea	7.3	15.0	45.0	37.0	2.5	3.0	25.8
Tanaidacea	—	—	—	—	0.4	0.4	<0.1
Isopoda	3.9	9.5	18.0	17.0	1.3	1.0	12.1
Amphipoda	280.0	118.2	952.9	1,269.3	133.7	17.1	655.8
Mysidacea	<0.1	0.2	10.6	1.0	—	<0.1	2.5
Decapoda	2.1	0.5	22.3	8.7	—	0.1	7.5
Unidentified	—	0.5	0.5	0.2	<0.1	—	0.3
BRYOZOA	16.3	6.9	27.9	21.9	0.4	—	15.7
BRACHIOPODA	22.4	9.5	—	—	<0.1	—	4.5
ECHINODERMATA	23.6	43.3	121.0	122.7	18.8	18.7	79.3
Crinoidea	—	<0.1	—	—	<0.1	—	<0.1
Holothuroidea	2.5	7.8	0.2	4.7	2.2	3.4	4.3
Echinoidea	3.6	4.6	105.6	21.8	0.2	0.3	29.3
Ophiuroidea	17.0	29.5	14.0	93.7	15.8	14.8	44.2
Asteroidea	0.4	1.5	1.1	2.5	0.6	0.2	1.5
HEMICHORDATA	—	—	—	0.3	—	0.1	0.1
CHORDATA	2.8	2.3	33.8	26.8	2.6	1.3	16.3
Ascidiacea	2.8	2.3	33.8	26.8	2.6	1.3	16.3
UNIDENTIFIED	1.7	4.9	4.3	7.6	9.4	7.2	5.8
Total	1,162.6	838.7	1,961.0	2,382.4	347.4	281.9	1,512.2

Table 7

The number of specimens of each taxon, expressed as a percentage of the total benthic invertebrate fauna, in relation to geographic area.

	Geographic areas						
Taxon	Nova Scotia	Gulf of Maine	Georges Bank	Southern New England Shelf	Georges Slope	Southern New England Slope	All areas
PORIFERA	0.4	0.3	<0.1	0.1	0.1	0.1	0.1
COELENTERATA	1.9	1.1	5.1	1.0	1.9	3.0	2.1
Hydrozoa	1.0	0.4	0.4	0.4.	<0.1	0.3	0.4
Anthozoa	0.9	0.7	4.7	0.6	1.9	2.7	1.7
Alcyonaria	0.1	0.1	—	<0.1	0.3	0.5	0.1
Zoantharia	0.7	0.4	4.7	0.3	0.9	1.5	1.5
Unidentified	0.2	0.2	<0.1	0.2	0.8	0.7	0.2
PLATYHELMINTHES	<0.1	<0.1	<0.1	<0.1	0.1	—	<0.1
Turbellaria	<0.1	<0.1	<0.1	<0.1	0.1	—	<0.1
NEMERTEA	0.3	0.5	1.2	0.3	0.3	0.6	0.5
ASCHELMINTHES	0.1	0.4	0.1	0.2	0.7	0.8	0.2
Nematoda	0.1	0.4	0.1	0.2	0.7	0.8	0.2
ANNELIDA	55.8	34.7	27.8	22.3	23.0	52.7	28.1
POGONOPHORA	<0.1	<0.1	—	—	0.9	1.9	<0.1
SIPUNCULIDA	0.8	0.6	0.2	0.3	0.3	3.1	0.4
ECHIURA	—	<0.1	—	<0.1	0.1	0.1	<0.1
PRIAPULIDA	—	—	—	—	<0.1	<0.1	<0.1
MOLLUSCA	6.6	36.5	2.4	10.2	23.9	20.5	12.4
Polyplacophora	0.2	0.4	<0.1	<0.1	0.2	0.1	0.1
Gastropoda	1.3	1.8	0.6	1.2	2.4	2.5	1.2
Bivalvia	4.4	32.9	1.8	8.9	20.0	16.3	10.8
Scaphopoda	0.8	1.4	0.1	<0.1	1.3	1.7	0.3
Cephalopoda	<0.1	—	<0.1	<0.1	<0.1	<0.1	<0.1
Unidentified	—	—	—	<0.1	<0.1	—	<0.1
ARTHROPODA	28.4	17.9	53.7	58.2	39.6	7.6	48.0
Pycnogonida	0.1	<0.1	<0.1	<0.1	<0.1	—	<0.1
Arachnida	—	—	<0.1	—	—	—	<0.1
Crustacea	28.3	17.9	53.7	58.2	39.6	7.6	48.0
Ostracoda	<0.1	<0.1	—	—	<0.1	<0.1	<0.1
Cirripedia	3.1	0.8	0.1	2.2	—	—	1.4
Copepoda	—	—	—	<0.1	—	0.1	<0.1
Cumacea	0.6	1.8	2.3	1.6	0.7	1.1	1.7
Tanaidacea	—	—	—	—	0.1	0.1	<0.1
Isopoda	0.3	1.1	0.9	0.7	0.4	0.4	0.8
Amphipoda	24.1	14.1	48.6	53.3	38.5	6.0	43.4
Mysidacea	<0.1	<0.1	0.5	<0.1	—	<0.1	0.2
Decapoda	0.2	0.1	1.1	0.4	—	<0.1	0.5
Unidentified	—	0.1	<0.1	<0.1	<0.1	—	<0.1
BRYOZOA	1.4	0.8	1.4	0.9	0.1	—	1.0
BRACHIOPODA	1.9	1.1	—	—	<0.1	—	0.3
ECHINODERMATA	2.0	5.2	6.2	5.2	5.4	6.6	5.2
Crinoidea	—	<0.1	—	—	<0.1	—	<0.1
Holothuroidea	0.2	0.9	<0.1	0.2	0.6	1.2	0.3
Echinoidea	0.3	0.5	5.4	0.9	<0.1	0.1	1.9
Ophiuroidea	1.5	3.5	0.7	3.9	4.6	5.2	2.9
Asteroidea	<0.1	0.2	<0.1	0.1	0.2	0.1	0.1
HEMICHORDATA	—	—	—	<0.1	—	<0.1	<0.1
CHORDATA	0.2	0.3	1.7	1.1	0.7	0.5	1.1
Ascidiacea	0.2	0.3	1.7	1.1	0.7	0.5	1.1
UNIDENTIFIED	0.1	0.6	0.2	0.3	2.7	2.5	0.4
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 8
Mean wet weight of specimens of each taxon (grams per square meter) in relation to geographic area.

Taxon	Geographic areas						
	Nova Scotia	Gulf of Maine	Georges Bank	Southern New England Shelf	Georges Slope	Southern New England Slope	All areas
PORIFERA	15.49	3.15	0.47	0.09	0.24	0.03	2.24
COELENTERATA	20.23	11.87	3.68	4.62	2.42	0.99	7.33
Hydrozoa	0.49	0.12	1.61	0.41	<0.01	0.03	0.52
Anthozoa	19.74	11.75	2.07	4.21	2.42	0.96	6.81
Alcyonaria	0.03	0.43	—	0.21	0.14	0.07	0.20
Zoantharia	19.54	10.90	2.04	3.84	1.90	0.70	6.39
Unidentified	0.16	0.41	0.03	0.15	0.38	0.19	0.22
PLATYHELMINTHES	<0.01	0.01	<0.01	0.01	0.01	—	0.01
Turbellaria	<0.01	0.01	<0.01	0.01	0.01	—	0.01
NEMERTEA	0.56	0.54	0.83	1.04	0.11	0.20	0.71
ASCHELMINTHES	<0.01	0.01	0.01	0.01	0.01	0.01	0.01
Nematoda	<0.01	0.01	0.01	0.01	0.01	0.01	0.01
ANNELIDA	18.50	15.51	7.93	29.60	4.86	4.32	17.41
POGONOPHORA	<0.01	<0.01	—	—	0.01	0.03	<0.01
SIPUNCULIDA	1.65	0.37	0.46	0.74	1.01	1.83	0.75
ECHIURA	—	0.01	—	0.07	5.18	0.40	0.03
PRIAPULIDA	—	—	—	—	0.01	0.05	<0.01
MOLLUSCA	54.40	31.59	79.54	170.90	2.65	1.18	83.64
Polyplacophora	0.10	0.19	<0.01	0.24	0.01	0.01	0.14
Gastropoda	2.47	0.90	1.98	4.29	0.32	0.05	2.23
Bivalvia	50.81	29.84	77.40	166.34	2.11	1.04	80.95
Scaphopoda	1.03	0.66	0.15	0.02	0.20	0.08	0.32
Cephalopoda	<0.01	—	0.01	0.01	<0.01	<0.01	0.01
Unidentified	—	—	—	<0.01	<0.01	—	<0.01
ARTHROPODA	16.49	2.43	9.75	17.11	0.64	0.13	9.41
Pycnogonida	0.02	0.02	<0.01	<0.01	<0.01	—	0.01
Arachnida	—	—	<0.01	—	—	—	<0.01
Crustacea	16.49	2.41	9.75	17.11	0.64	0.13	9.40
Ostracoda	<0.01	<0.01	—	—	<0.01	<0.01	<0.01
Cirripedia	12.71	0.47	0.35	6.84	—	—	3.39
Copepoda	—	—	—	<0.01	—	<0.01	<0.01
Cumacea	0.03	0.05	0.20	0.17	0.04	0.02	0.11
Tanaidacea	—	—	—	—	0.01	<0.01	<0.01
Isopoda	0.09	0.34	0.30	0.40	0.02	0.02	0.29
Amphipoda	1.36	0.94	5.55	8.34	0.57	0.08	4.16
Mysidacea	<0.01	<0.01	0.05	0.01	—	<0.01	0.01
Decapoda	2.27	0.61	3.29	1.36	—	0.02	1.43
Unidentified	—	<0.01	<0.01	<0.01	<0.01	—	<0.01
BRYOZOA	6.32	0.17	2.64	0.71	0.02	—	1.29
BRACHIOPODA	3.68	2.12	—	—	<0.01	—	0.89
ECHINODERMATA	39.44	56.42	119.99	36.06	3.89	10.01	55.00
Crinoidea	—	<0.01	—	—	<0.01	—	<0.01
Holothuroidea	0.77	27.55	0.50	14.65	1.28	2.75	12.87
Echinoidea	32.75	23.54	117.19	12.89	1.77	4.62	36.75
Ophiuroidea	1.46	3.30	1.26	5.41	0.79	2.62	3.26
Asteroidea	4.45	2.03	1.04	3.11	0.05	0.02	2.13
HEMICHORDATA	—	—	—	0.05	—	<0.01	0.02
CHORDATA	0.79	2.62	8.41	5.13	0.17	0.11	4.10
Ascidiacea	0.79	2.62	8.41	5.13	0.17	0.11	4.10
UNIDENTIFIED	0.12	0.23	0.08	0.52	0.12	0.17	0.27
Total	177.64	127.03	233.79	266.64	21.34	19.46	183.39

Table 9

The wet weight of specimens of each taxon, expressed as a percentage of the total benthic invertebrate fauna, in relation to geographic area.

	Geographic areas						
Taxon	Nova Scotia	Gulf of Maine	Georges Bank	Southern New England Shelf	Georges Slope	Southern New England Slope	All areas
PORIFERA	8.7	2.5	0.2	0.1	1.1	0.2	1.2
COELENTERATA	11.4	9.4	1.6	1.7	11.3	5.1	4.0
Hydrozoa	0.3	0.1	0.7	0.2	<0.1	0.2	0.3
Anthozoa	11.1	9.3	0.9	1.5	11.3	4.9	3.7
Alcyonaria	<0.1	0.3	—	0.1	0.7	0.4	0.1
Zoantharia	11.0	8.6	0.9	1.4	8.9	3.6	3.5
Unidentified	0.1	0.3	<0.1	0.1	1.8	1.0	0.1
PLATYHELMINTHES	<0.1	<0.1	<0.1	<0.1	0.1	—	<0.1
Turbellaria	<0.1	<0.1	<0.1	<0.1	0.1	—	<0.1
NEMERTEA	0.3	0.4	0.4	0.4	0.5	1.0	0.4
ASCHELMINTHES	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Nematoda	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
ANNELIDA	10.4	12.2	3.4	11.1	22.8	22.2	9.5
POGONOPHORA	<0.1	<0.1	—	—	<0.1	0.2	<0.1
SIPUNCULIDA	0.9	0.3	0.2	0.3	4.7	9.4	0.4
ECHIURA	—	<0.1	—	<0.1	24.3	2.0	0.2
PRIAPULIDA	—	—	—	—	0.1	0.2	<0.1
MOLLUSCA	30.6	24.9	34.0	64.1	12.4	6.0	45.6
Polyplacophora	0.1	0.2	<0.1	0.1	0.1	<0.1	0.1
Gastropoda	1.4	0.7	0.8	1.6	1.5	0.3	1.2
Bivalvia	28.6	23.5	33.1	62.4	9.9	5.3	44.1
Scaphopoda	0.6	0.5	0.1	<0.1	0.9	0.4	0.2
Cephalopoda	<0.1	—	<0.1	<0.1	<0.1	<0.1	<0.1
Unidentified	—	—	—	<0.1	<0.1	—	<0.1
ARTHROPODA	9.3	1.9	4.2	6.4	3.0	0.6	5.1
Pycnogonida	<0.1	<0.1	<0.1	<0.1	<0.1	—	<0.1
Arachnida	—	—	<0.1	—	—	—	<0.1
Crustacea	9.3	1.9	4.2	6.4	3.0	0.6	5.1
Ostracoda	<0.1	<0.1	—	—	<0.1	<0.1	<0.1
Cirripedia	7.2	0.4	0.2	2.6	—	—	1.8
Copepoda	—	—	—	<0.1	—	<0.1	<0.1
Cumacea	<0.1	<0.1	0.1	0.1	0.2	0.1	0.1
Tanaidacea	—	—	—	—	<0.1	<0.1	<0.1
Isopoda	<0.1	0.3	0.1	0.2	0.1	0.1	0.2
Amphipoda	0.8	0.7	2.4	3.1	2.7	0.4	2.3
Mysidacea	<0.1	<0.1	<0.1	<0.1	—	<0.1	<0.1
Decapoda	1.3	0.5	1.4	0.5	—	0.1	0.8
Unidentified	—	<0.1	<0.1	<0.1	<0.1	—	<0.1
BRYOZOA	3.6	0.1	1.1	0.3	0.1	—	0.7
BRACHIOPODA	2.1	1.7	—	—	<0.1	—	0.5
ECHINODERMATA	22.2	44.4	51.3	13.5	18.2	51.5	30.0
Crinoidea	—	<0.1	—	—	<0.1	—	<0.1
Holothuroidea	0.4	21.7	0.2	5.5	6.0	14.2	7.0
Echinoidea	18.4	18.5	50.1	4.8	8.3	23.7	20.0
Ophiuroidea	0.8	2.6	0.5	2.0	3.7	13.5	1.8
Asteroidea	2.5	1.6	0.4	1.2	0.2	0.1	1.2
HEMICHORDATA	—	—	—	<0.1	—	<0.1	<0.1
CHORDATA	0.4	2.1	3.6	1.9	0.8	0.6	2.2
Ascidiacea	0.4	2.1	3.6	1.9	0.8	0.6	2.2
UNIDENTIFIED	0.1	0.2	<0.1	0.2	0.6	0.9	0.2
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 10
Frequency of occurrence (%) of each taxonomic group in the samples in each geographic area.

Taxon	Geographic areas					
	Nova Scotia	Gulf of Maine	Georges Bank	Southern New England Shelf	Georges Slope	Southern New England Slope
PORIFERA	19	9	4	3	10	5
COELENTERATA	61	33	39	43	64	46
Hydrozoa	29	8	15	13	4	1
Anthozoa	32	25	24	30	60	45
Alcyonaria	4	3	—	7	27	17
Zoantharia	31	22	28	25	17	21
PLATYHELMINTHES	2	<1	1	3	2	—
Turbellaria	2	<1	1	3	2	—
NEMERTEA	28	32	32	52	35	25
ASCHELMINTHES	8	9	5	6	39	15
Nematoda	8	9	5	6	39	15
ANNELIDA	97	98	89	99	96	99
POGONOPHORA	2	1	—	—	35	42
SIPUNCULIDA	42	20	13	24	25	36
ECHIURA	—	<1	—	1	15	7
PRIAPULIDA	—	—	—	—	4	3
MOLLUSCA	91	90	73	92	92	95
Polyplacophora	24	11	1	5	15	6
Gastropoda	54	43	35	43	58	53
Bivalvia	80	87	64	89	89	94
Scaphopoda	46	35	7	4	35	33
Cephalopoda	1	—	<1	<1	2	1
ARTHROPODA	95	71	100	95	85	74
Pycnogonida	8	1	3	2	6	—
Arachnida	—	—	1	—	—	—
Crustacea	95	71	100	95	85	74
Ostracoda	2	<1	—	—	2	1
Cirripedia	15	4	2	4	—	—
Copepoda	—	—	—	1	—	3
Cumacea	31	24	44	49	31	19
Tanaidacea	—	—	—	—	15	9
Isopoda	35	21	48	48	29	20
Amphipoda	94	58	94	92	73	63
Mysidacea	1	1	10	4	--	1
Decapoda	18	6	46	33	—	3
BRYOZOA	19	12	13	11	6	—
BRACHIOPODA	21	12	—	—	2	—
ECHINODERMATA	69	79	67	67	81	75
Crinoidea	—	<1	—	—	2	—
Holothuroidea	22	25	2	17	40	27
Echinoidea	26	19	51	28	8	9
Ophiuroidea	55	64	22	35	62	59
Asteroidea	9	13	9	19	14	6
HEMICHORDATA	—	—	—	1	—	1
CHORDATA	20	12	14	23	14	16
Ascidiacea	20	12	14	23	14	16

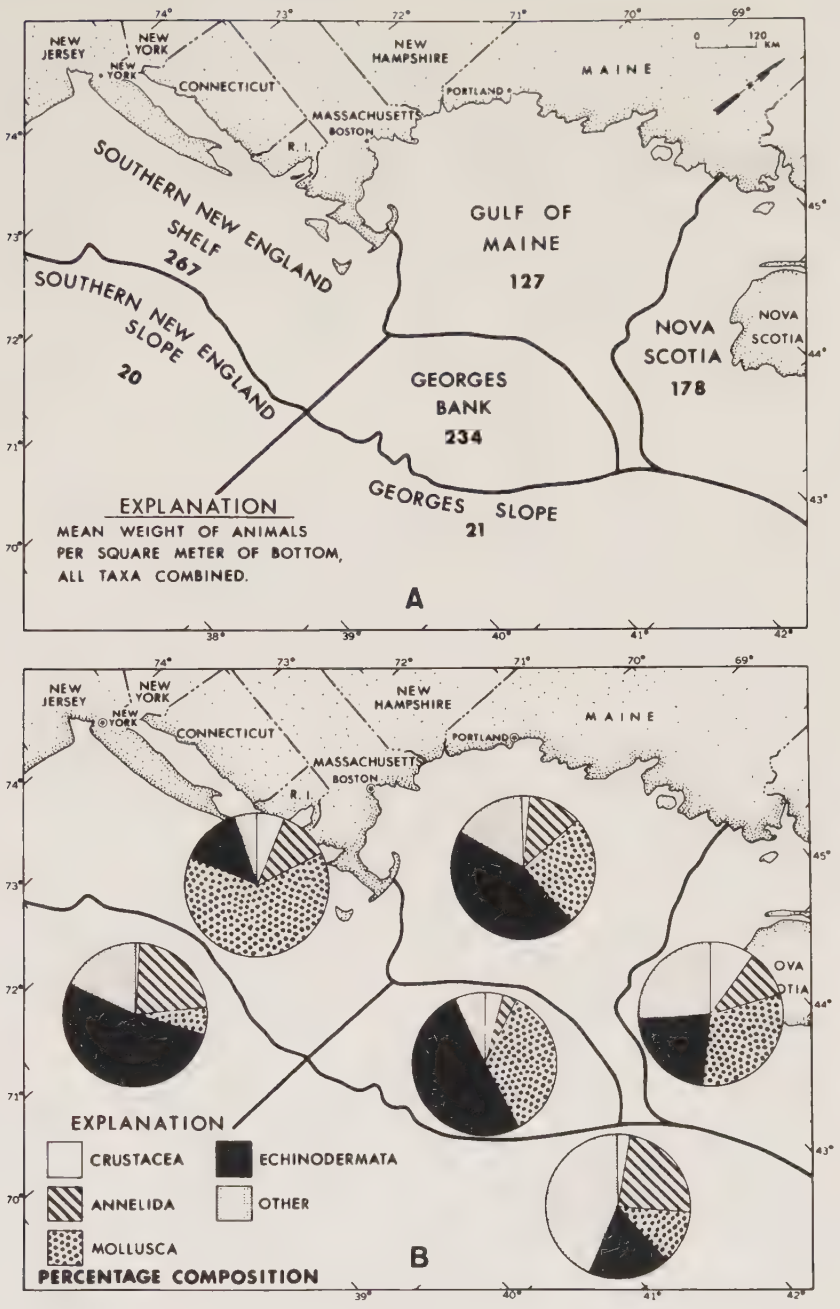


Figure 14

Quantitative composition of the total macrobenthic- invertebrate fauna in relation to the six standard geographic subareas. A.—Mean wet weight of animals per square meter of bottom area; B.—Percentage composition, by biomass, of the major taxonomic groups.

A gradient was evident in the density distribution. In the three shallow water areas—Nova Scotia, Georges Bank, and Southern New England Shelf—average density increased in the order listed from the northeast to the southwest. The Southern New England Shelf area (2,382/m^2) had about twice the density of the Nova Scotian area (1,163/m^2). The Gulf of Maine averaged 839/m^2, and the two slope areas had average densities of about 300/m^2.

Biomass distribution followed precisely the same rank order as density, and the magnitudes of differences in biomass from one area to another were roughly the

Table 11
Mean number of specimens of each taxon per square meter in relation to water depth.

Taxon	Water depth (m)								
	0–24	25–49	50–99	100–199	200–499	500–599	1,000–1,999	2,000–3,999	All depths
PORIFERA	1.3	2.8	0.8	1.3	2.5	0.3	0.3	0.1	1.5
COELENTERATA	56.7	96.8	28.6	11.6	9.0	6.0	4.3	1.6	32.1
Hydrozoa	36.8	5.1	5.9	2.5	1.0	—	0.1	0.1	6.4
Anthozoa	19.9	91.7	22.7	9.1	8.0	6.0	4.2	1.5	25.7
Alcyonaria	—	—	0.9	0.9	1.9	1.1	1.2	0.4	0.8
Zoantharia	5.6	91.3	21.1	6.8	4.4	2.0	0.4	0.2	22.6
Unidentified	14.3	0.4	0.7	1.4	1.7	2.9	2.7	1.0	2.2
PLATYHELMINTHES	2.6	<0.1	0.3	—	0.2	—	—	—	0.4
Turbellaria	2.6	<0.1	0.3	—	0.2	—	—	—	0.4
NEMERTEA	4.2	27.2	7.8	3.8	3.4	0.5	1.5	0.7	8.2
ASCHELMINTHES	6.8	0.8	3.2	1.4	4.4	4.2	1.4	1.7	2.8
Nematoda	6.8	0.8	3.2	1.4	4.4	4.2	1.4	1.7	2.8
ANNELIDA	719.3	436.8	51.9	455.9	240.6	106.5	30.2	9.1	425.0
POGONOPHORA	—	—	—	0.1	1.3	6.8	3.2	3.5	0.6
SIPUNCULIDA	1.8	5.8	6.2	7.5	8.1	1.5	0.7	1.2	5.9
ECHIURA	0.3	—	—	0.2	—	—	0.5	0.6	0.1
PRIAPULIDA	—	—	—	—	—	—	0.2	0.1	<0.1
MOLLUSCA	570.2	205.0	197.3	135.7	91.0	121.5	55.7	27.2	188.0
Polyplacophora	0.8	4.0	1.1	0.4	2.5	0.2	0.5	0.2	1.5
Gastropoda	64.1	18.4	15.2	11.3	12.1	23.7	3.9	1.1	17.8
Bivalvia	505.1	182.2	179.2	113.1	62.6	86.7	50.1	25.8	163.1
Scaphopoda	0.2	0.4	1.5	9.5	13.8	10.8	1.2	0.1	5.1
Cephalopoda	—	—	—	1.5	0.1	—	—	—	0.4
Unidentified	—	—	0.3	—	—	0.1	—	—	0.1
ARTHROPODA	1,039.4	1,255.7	1,351.6	168.8	67.0	14.6	13.2	6.6	726.2
Pycnogonida	0.6	0.6	0.3	0.5	—	0.2	0.1	—	0.3
Arachnida	—	—	<0.1	—	—	—	—	—	<0.1
Crustacea	1,038.8	1,255.1	1,351.3	168.3	67.0	14.4	13.1	6.6	725.9
Ostracoda	—	—	<0.1	<0.1	0.1	0.1	—	0.1	<0.1
Cirripedia	214.2	13.7	2.9	2.3	0.7	—	—	—	21.8
Copepoda	—	—	<0.1	—	<0.1	0.5	—	—	<0.1
Cumacea	33.1	39.8	50.3	6.8	2.9	1.6	0.7	1.7	25.8
Tanaidacea	—	—	—	—	0.1	—	0.1	1.0	<0.1
Isopoda	22.4	37.9	11.1	2.9	3.1	1.3	0.4	1.9	12.1
Amphipoda	746.4	1,148.6	1,273.8	147.4	59.1	11.1	12.0	2.9	655.8
Mysidacea	4.0	6.5	3.8	0.1	<0.1	—	—	—	2.5
Decapoda	18.0	8.2	9.1	8.6	0.3	—	0.1	—	7.5
Unidentified	0.6	0.4	0.2	0.2	0.8	—	—	—	0.3
BRYOZOA	38.6	29.4	18.9	7.8	4.3	—	—	0.5	15.7
BRACHIOPODA	—	—	1.2	6.5	17.0	0.1	—	—	4.5
ECHINODERMATA	47.4	133.2	87.4	94.6	48.1	6.5	4.4	7.3	79.3
Crinoidea	—	—	—	—	0.1	—	0.1	—	<0.1
Holothuroidea	1.5	1.3	4.9	4.0	9.8	1.2	1.9	0.7	4.3
Echinoidea	44.4	127.4	19.1	2.0	2.6	—	0.1	0.3	29.3
Ophiuroidea	0.8	2.0	61.5	86.7	35.0	5.2	2.0	6.2	44.2
Asteroidea	0.7	2.5	1.9	1.8	0.5	0.1	0.3	0.1	1.5
HEMICHORDATA	—	—	0.3	<0.1	—	0.5	—	—	0.1
CHORDATA	9.0	32.0	29.8	6.2	2.7	0.1	1.0	1.7	16.3
Ascidiacea	9.0	32.0	29.8	6.2	2.7	0.1	1.0	1.7	16.3
UNIDENTIFIED	6.0	6.6	5.1	5.3	5.6	3.5	5.8	13.1	5.8
Total	2,503.3	2,232.0	2,256.9	906.6	505.1	272.4	122.2	74.9	1,512.2

Table 12

The number of specimens of each taxon, expressed as a percentage of the total benthic invertebrate fauna, in relation to water depth.

	Depth zones (m)								
Taxon	0–24	25–49	50–99	100–199	200–499	500–599	1,000–1,999	2,000–3,999	All depths
PORIFERA	0.1	0.1	<0.1	0.2	0.5	0.1	0.2	0.1	0.1
COELENTERATA	2.3	4.3	1.3	1.3	1.8	2.2	3.5	2.1	2.1
Hydrozoa	1.5	0.2	0.3	0.3	0.2	—	<0.1	0.1	0.4
Anthozoa	0.8	4.1	1.0	1.0	1.6	2.2	3.5	2.0	1.7
Alcyonaria	—	—	<0.1	0.1	0.4	0.4	1.0	0.6	0.1
Zoantharia	0.2	4.1	0.9	0.8	0.9	0.7	0.3	0.2	1.5
Unidentified	0.6	<0.1	<0.1	0.2	0.3	1.0	2.2	1.3	0.2
PLATYHELMINTHES	0.1	<0.1	<0.1	—	<0.1	—	—	—	<0.1
Turbellaria	0.1	<0.1	<0.1	—	<0.1	—	—	—	<0.1
NEMERTEA	0.2	1.2	0.4	0.4	0.7	0.2	1.2	0.9	0.5
ASCHELMINTHES	0.3	<0.1	0.1	0.2	0.9	1.5	1.1	2.3	0.2
Nematoda	0.3	<0.1	0.1	0.2	0.9	1.5	1.1	2.3	0.2
ANNELIDA	28.7	19.6	23.0	50.3	47.6	39.1	24.7	12.2	28.1
POGONOPHORA	—	—	—	<0.1	0.2	2.5	2.6	4.6	<0.1
SIPUNCULIDA	0.1	0.3	0.3	0.8	1.6	0.5	0.6	1.6	0.4
ECHIURA	<0.1	—	—	<0.1	—	—	0.4	0.8	<0.1
PRIAPULIDA	—	—	—	—	—	—	0.2	0.1	<0.1
MOLLUSCA	22.8	9.2	8.7	15.0	18.0	44.6	45.6	36.3	12.4
Polyplacophora	<0.1	0.2	<0.1	<0.1	0.5	0.1	0.4	0.3	0.1
Gastropoda	2.6	0.8	0.7	1.2	2.4	8.7	3.2	1.5	1.2
Bivalvia	20.2	8.2	7.9	12.5	12.4	31.8	41.0	34.4	10.8
Scaphopoda	<0.1	<0.1	0.1	1.0	2.7	4.0	1.0	0.1	0.3
Cephalopoda	—	—	—	0.2	<0.1	—	—	—	<0.1
Unidentified	—	—	<0.1	—	—	<0.1	—	—	<0.1
ARTHROPODA	41.5	56.3	59.9	18.6	13.3	5.4	10.8	8.8	48.0
Pycnogonida	<0.1	<0.1	<0.1	<0.1	—	0.1	<0.1	—	<0.1
Arachnida	—	—	<0.1	—	—	—	—	—	<0.1
Crustacea	41.5	56.2	59.9	18.6	13.3	5.3	10.8	8.8	48.0
Ostracoda	—	—	<0.1	<0.1	<0.1	<0.1	—	0.1	<0.1
Cirripedia	8.6	0.6	0.1	0.2	0.1	—	—	—	1.4
Copepoda	—	—	<0.1	—	<0.1	0.2	—	—	<0.1
Cumacea	1.3	1.8	2.2	0.8	0.6	0.6	0.6	2.3	1.7
Tanaidacea	—	—	—	—	<0.1	—	<0.1	1.4	<0.1
Isopoda	0.9	1.7	0.5	0.3	0.6	0.5	0.3	2.5	0.8
Amphipoda	29.8	51.5	56.4	16.3	11.7	4.1	9.8	3.9	43.4
Mysidacea	0.2	0.3	0.2	<0.1	<0.1	—	—	—	0.2
Decapoda	0.7	0.4	0.4	1.0	0.1	—	<0.1	—	0.5
Unidentified	<0.1	<0.1	<0.1	<0.1	0.2	—	—	0.1	<0.1
BRYOZOA	1.5	1.3	0.8	0.9	0.8	—	—	0.7	1.0
BRACHIOPODA	—	—	<0.1	0.7	3.4	<0.1	—	—	0.3
ECHINODERMATA	1.9	6.0	3.9	10.4	9.5	2.4	3.6	9.8	5.2
Crinoidea	—	—	—	—	<0.1	—	<0.1	—	<0.1
Holothuroidea	0.1	0.1	0.2	0.4	1.9	0.4	1.5	0.9	0.3
Echinoidea	1.8	5.7	0.8	0.2	0.5	—	0.1	0.4	1.9
Ophiuroidea	<0.1	0.1	2.7	9.6	6.9	1.9	1.6	8.3	2.9
Asteroidea	<0.1	0.1	0.1	0.2	0.1	<0.1	0.3	0.1	0.1
HEMICHORDATA	—	—	<0.1	<0.1	—	0.2	—	—	<0.1
CHORDATA	0.4	1.4	1.3	0.7	0.5	<0.1	0.8	2.2	1.1
Ascidiacea	0.4	1.4	1.3	0.7	0.5	<0.1	0.8	2.2	1.1
UNIDENTIFIED	0.2	0.3	0.2	0.6	1.1	1.3	4.7	17.4	0.4
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

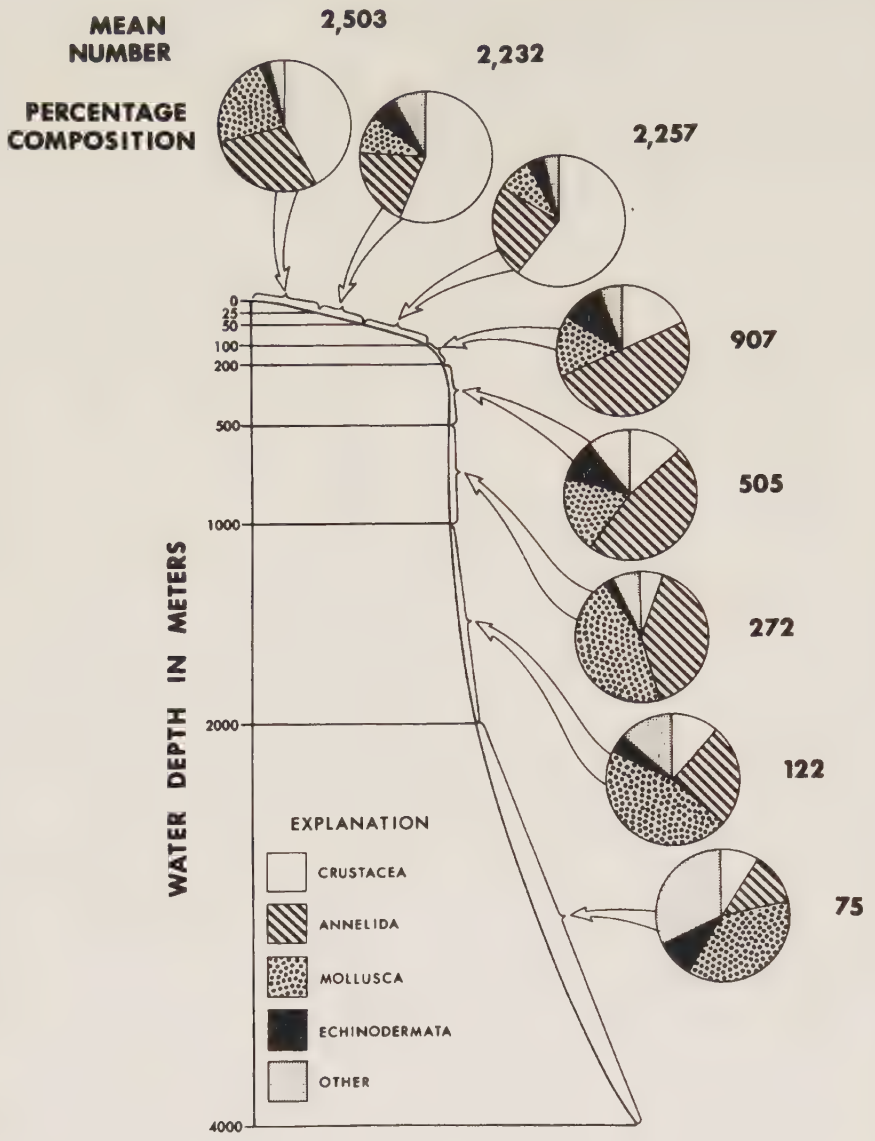


Figure 15

Quantitative composition of the total macrobenthic invertebrate fauna in relation to water depth. Mean number of individuals per square meter of bottom area, and percentage composition, by density, of the major taxonomic groups are shown.

same as the changes in density (Tables 8, 9; Fig. 14A). Southern New England Shelf and Georges Bank had the highest average biomasses (267 and 234 g/m^2); biomass was intermediate (178 and 127 g/m^2) in Nova Scotia and the Gulf of Maine, and low (21 and 20 g/m^2) on Georges Slope and Southern New England Slope.

The percentage occurrence of each taxonomic group in the samples in each geographic area is presented in Table 10.

Bathymetric Distribution

One of the most striking relationships in the New England region was the pronounced diminution in quantity of macrobenthic invertebrates from shallow to deep water (Tables 11, 12; Fig. 15). In the shallowest waters sampled (0–24 m) the average density was 2,503/m^2, whereas in the deepest water (2,000–3,999 m) the density averaged only 75/m^2. The decrease from one depth range to an-

Table 13
Mean wet weight of specimens of each taxon (grams per square meter) in relation to water depth.

Taxon	Water depth (m)								
	0–24	25–49	50–99	100–199	200–499	500–599	1,000–1,999	2,000–3,999	All depths
PORIFERA	0.06	1.23	2.90	3.08	3.12	0.54	0.02	0.03	2.24
COELENTERATA	3.63	1.49	3.38	18.95	9.13	0.36	0.72	0.69	7.33
Hydrozoa	1.21	0.22	1.17	0.16	0.02	—	<0.01	<0.01	0.52
Anthozoa	2.42	1.27	2.21	18.79	9.11	0.36	0.72	0.69	6.81
Alcyonaria	—	—	0.16	0.33	0.47	0.04	0.25	0.01	0.20
Zoantharia	2.08	1.22	1.99	18.28	8.05	0.19	0.18	0.19	6.39
Unidentified	0.35	0.05	0.06	0.18	0.59	0.13	0.29	0.49	0.22
PLATYHELMINTHES	0.02	<0.01	0.01	—	<0.01	—	—	—	0.01
Turbellaria	0.02	<0.01	0.01	—	<0.01	—	—	—	0.01
NEMERTEA	1.00	1.44	0.99	0.23	0.40	0.01	0.06	0.12	0.71
ASCHELMINTHES	<0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Nematoda	<0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
ANNELIDA	27.22	16.24	25.20	14.76	10.70	4.76	1.41	0.76	17.41
POGONOPHORA	—	—	—	<0.01	0.01	0.03	0.02	0.01	<0.01
SIPUNCULIDA	0.22	0.57	0.82	0.77	0.54	3.93	1.38	0.53	0.75
ECHIURA	0.22	—	—	0.01	—	—	5.04	3.52	0.30
PRIAPULIDA	—	—	—	—	—	—	0.12	0.01	<0.01
MOLLUSCA	257.88	106.89	132.14	20.67	10.80	3.26	1.44	0.58	83.64
Polyplacophora	0.84	0.07	0.02	0.02	0.29	0.01	0.01	<0.01	0.14
Gastropoda	4.85	1.82	4.23	1.07	0.18	0.29	0.15	0.17	2.23
Bivalvia	252.18	104.94	127.80	18.56	10.04	2.79	1.07	0.41	80.95
Scaphopoda	<0.01	0.07	0.09	0.98	0.29	0.17	0.22	<0.01	0.32
Cephalopoda	—	—	—	0.03	<0.01	—	—	—	0.01
Unidentified	—	—	<0.01	—	—	0.01	—	—	<0.01
ARTHROPODA	37.04	15.64	9.31	2.40	3.89	0.09	0.08	0.10	9.41
Pycnogonida	0.01	<0.01	<0.01	0.03	—	<0.01	<0.01	—	0.01
Arachnida	—	—	<0.01	—	—	—	—	—	<0.01
Crustacea	37.03	15.64	9.31	2.37	3.89	0.09	0.08	0.10	9.40
Ostracoda	—	—	<0.01	<0.01	<0.01	<0.01	—	<0.01	<0.01
Cirripedia	27.08	3.89	0.29	0.10	2.53	—	—	—	3.39
Copepoda	—	—	<0.01	—	<0.01	0.10	—	—	<0.01
Cumacea	0.08	0.11	0.26	0.04	0.02	0.01	0.01	0.05	0.11
Tanaidacea	—	—	—	—	<0.01	—	<0.01	0.01	<0.01
Isopoda	0.15	0.66	0.27	0.15	0.42	0.02	0.01	0.02	0.29
Amphipoda	6.39	9.77	6.38	0.97	0.31	0.06	0.03	0.02	4.16
Mysidacea	0.03	0.02	0.02	<0.01	<0.01	—	—	—	0.01
Decapoda	3.32	1.19	2.10	1.12	0.61	—	0.03	—	1.43
Unidentified	0.01	<0.01	<0.01	<0.01	<0.01	—	—	<0.01	<0.01
BRYOZOA	0.96	0.92	2.88	0.87	0.14	—	—	0.02	1.29
BRACHIOPODA	—	—	0.11	1.05	3.98	0.01	—	—	0.89
ECHINODERMATA	105.93	166.80	33.95	34.23	19.18	1.72	3.16	4.62	55.00
Crinoidea	—	—	—	—	<0.01	—	<0.01	—	<0.01
Holothuroidea	36.59	12.76	19.23	6.47	3.57	0.24	1.24	2.15	12.87
Echinoidea	65.74	153.88	9.24	16.16	11.11	—	1.13	1.78	36.75
Ophiuroidea	0.29	0.06	2.49	7.50	4.49	1.48	0.75	0.66	3.26
Asteroidea	3.30	0.11	2.99	4.10	0.01	<0.01	0.04	0.04	2.13
HEMICHORDATA	—	—	0.05	0.01	—	0.01	—	—	0.02
CHORDATA	3.85	5.20	8.93	1.03	0.72	<0.01	<0.01	0.21	4.10
Ascidiacea	3.85	5.20	8.93	1.03	0.72	<0.01	<0.01	0.21	4.10
UNIDENTIFIED	0.19	0.58	0.28	0.23	0.12	0.19	0.23	0.15	0.27
Total	438.26	317.01	220.95	98.30	62.72	14.91	13.66	11.36	183.39

Table 14

The wet weight of specimens of each taxon, expressed as a percentage of the total benthic invertebrate fauna, in relation to water depth.

Taxon	Depth zones (m)								
	0–24	25–49	50–99	100–199	200–499	500–599	1,000–1,999	2,000–3,999	All depths
PORIFERA	<0.1	0.4	1.3	3.1	5.0	3.6	0.1	0.3	1.2
COELENTERATA	0.8	0.5	1.5	19.3	14.6	2.4	5.3	6.1	4.0
Hydrozoa	0.3	0.1	0.5	0.2	<0.1	—	<0.1	<0.1	0.3
Anthozoa	0.5	0.4	1.0	19.1	14.6	2.4	5.3	6.1	3.7
Alcyonaria	—	—	0.1	0.3	0.8	0.3	1.8	0.1	0.1
Zoantharia	0.5	0.4	0.9	18.6	12.8	1.2	1.3	1.7	3.5
Unidentified	0.1	<0.1	<0.1	0.2	0.9	0.9	2.1	4.3	0.1
PLATYHELMINTHES	<0.1	<0.1	<0.1	—	<0.1	—	—	—	<0.1
Turbellaria	<0.1	<0.1	<0.1	—	<0.1	—	—	—	<0.1
NEMERTEA	0.2	0.5	0.4	0.2	0.6	0.1	0.4	1.0	0.4
ASCHELMINTHES	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	0.1	0.1	<0.1
Nematoda	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	0.1	0.1	<0.1
ANNELIDA	6.2	5.1	11.4	15.0	7.0	32.0	10.3	6.7	9.5
POGONOPHORA	—	—	—	<0.1	<0.1	0.2	0.1	0.1	<0.1
SIPUNCULIDA	<0.1	0.2	0.4	0.8	0.8	26.3	10.1	4.7	0.4
ECHIURA	0.1	—	—	<0.1	—	—	36.9	31.0	0.2
PRIAPULIDA	—	—	—	—	—	—	0.9	0.1	<0.1
MOLLUSCA	58.8	33.7	59.8	21.0	17.2	21.9	10.6	5.1	45.6
Polyplacophora	0.2	<0.1	<0.1	<0.1	0.5	<0.1	<0.1	<0.1	0.1
Gastropoda	1.1	0.6	1.9	1.1	0.3	1.9	1.1	1.5	1.2
Bivalvia	57.5	33.1	57.8	18.9	16.0	18.7	7.8	3.6	44.1
Scaphopoda	<0.1	<0.1	<0.1	1.0	0.5	1.2	1.6	<0.1	0.2
Cephalopoda	—	—	—	<0.1	<0.1	—	—	—	<0.1
Unidentified	—	—	<0.1	—	—	0.1	—	—	<0.1
ARTHROPODA	8.4	4.9	4.2	2.4	6.2	0.6	0.6	0.9	5.1
Pycnogonida	<0.1	<0.1	<0.1	<0.1	—	<0.1	<0.1	—	<0.1
Arachnida	—	—	<0.1	—	—	—	—	—	<0.1
Crustacea	8.4	4.9	4.2	2.4	6.2	0.6	0.6	0.9	5.1
Ostracoda	—	—	<0.1	<0.1	<0.1	<0.1	—	<0.1	<0.1
Cirripedia	6.2	1.2	0.1	0.1	4.0	—	—	—	1.8
Copepoda	—	—	<0.1	—	<0.1	<0.1	—	—	<0.1
Cumacea	<0.1	<0.1	0.1	<0.1	<0.1	0.1	0.1	0.4	0.1
Tanaidacea	—	—	—	—	<0.1	—	<0.1	0.1	<0.1
Isopoda	<0.1	0.2	0.1	0.2	0.7	0.1	<0.1	0.2	0.2
Amphipoda	1.5	3.1	2.9	1.0	0.5	0.4	0.2	0.2	2.3
Mysidacea	<0.1	<0.1	<0.1	<0.1	<0.1	—	—	—	<0.1
Decapoda	0.8	0.4	1.0	1.1	1.0	—	0.2	—	0.8
Unidentified	<0.1	<0.1	<0.1	<0.1	<0.1	—	—	<0.1	<0.1
BRYOZOA	0.2	0.3	1.3	0.9	0.2	—	—	0.2	0.7
BRACHIOPODA	—	—	<0.1	1.1	6.3	<0.1	—	—	0.5
ECHINODERMATA	24.2	52.6	15.4	34.8	30.6	11.5	23.0	40.7	30.0
Crinoidea	—	—	—	—	<0.1	—	<0.1	—	<0.1
Holothuroidea	8.4	4.0	8.7	6.6	5.7	1.6	9.0	18.9	7.0
Echinoidea	15.0	48.5	4.2	16.4	17.7	—	8.2	15.7	20.0
Ophiuroidea	0.1	<0.1	1.1	7.6	7.2	9.9	5.5	5.8	1.8
Asteroidea	0.8	<0.1	1.4	4.2	<0.1	<0.1	0.3	0.3	1.2
HEMICHORDATA	—	—	<0.1	1.0	—	<0.1	—	—	<0.1
CHORDATA	0.9	1.6	4.0	1.0	1.2	<0.1	<0.1	1.8	2.2
Ascidiacea	0.9	1.6	4.0	1.0	1.2	<0.1	<0.1	1.8	2.2
UNIDENTIFIED	<0.1	0.2	0.1	0.2	0.2	1.3	1.6	1.3	0.2
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

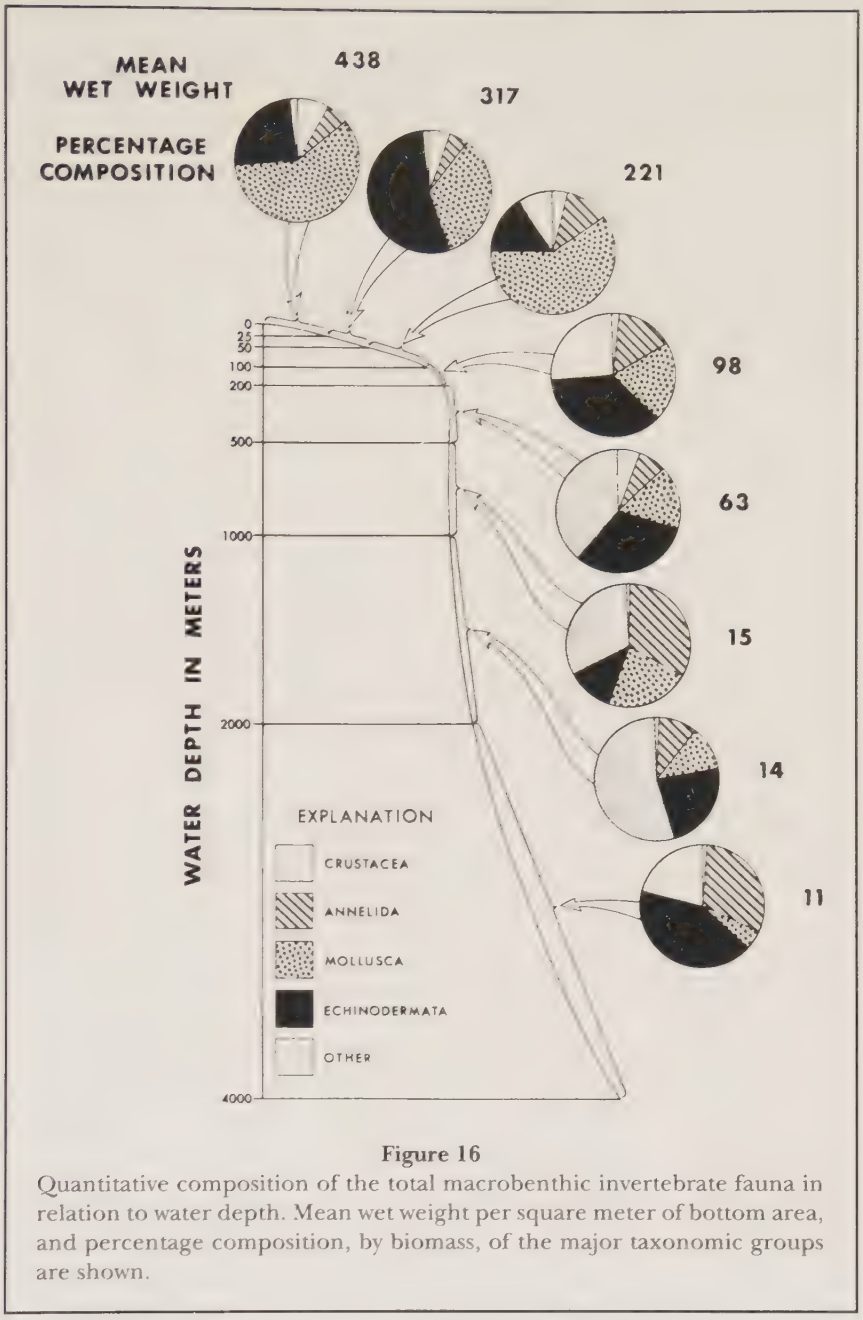


Figure 16

Quantitative composition of the total macrobenthic invertebrate fauna in relation to water depth. Mean wet weight per square meter of bottom area, and percentage composition, by biomass, of the major taxonomic groups are shown.

other was not uniform over the entire depth spectrum. There was a 60% drop in density from 50–99 m to 100–199 m and the largest drop in density occurred between 100 and 200 m depth.. Another way of expressing this change is to say there was a decrease in density per meter increase in depth. In the vicinity of 100 m the average density decreased by 18 specimens with each 1-m increase in water depth. In shallower water the rate of decrease was as high as 10 specimens per 1 m of water depth increase, but the percentage change was substantially lower. In deep water (below 200 m) the diminution rate was less than one specimen per meter change in water depth. Differences in density in depth ranges between 1,000 and 1,999 m and between 2,000 and 3,999 m decreased an average of 0.05 per meter increase in depth.

Biomass diminished with depth from an average of 438 g/m^2 in shallow water to 11 g/m^2 on the continental rise (Tables 13, 14; Fig. 16). The biomass remained rather high (221 g or more) in shallow water out to 100 meters. In the vicinity of 100 m the biomass was 56% lower than in the shallowest water, and 76% lower in the vicinity of 500 m depth.

The relatively high biomass, averaging 11 g/m^2, at water depths between 2,000 and 3,999 m was due in

Table 15
Frequency of occurrence (%) of each taxonomic group in the samples in each depth range class.

Taxon	Water depth (m)							
	0–24	25–49	50–99	100–199	200–499	500–599	1,000–1,999	2,000–3,999
PORIFERA	5	3	5	8	12	9	12	3
COELENTERATA	36	36	50	40	33	46	65	41
Hydrozoa	21	16	15	10	4	—	3	3
Anthozoa	15	20	35	30	29	46	62	38
Alcyonaria	—	—	5	5	8	23	29	22
Zoantharia	16	21	33	29	19	9	18	8
PLATYHELMINTHES	2	1	4	—	1	—	—	—
Turbellaria	2	1	4	—	1	—	—	—
NEMERTEA	35	51	47	30	28	18	33	24
ASCHELMINTHES	2	6	8	5	15	32	18	35
Nematoda	2	6	8	5	15	32	18	35
ANNELIDA	96	93	96	98	97	100	97	95
POGONOPHORA	—	—	—	1	5	50	53	43
SIPUNCULIDA	3	13	26	32	25	32	21	22
ECHIURA	2	—	—	<1	—	—	21	19
PRIAPULIDA	—	—	—	—	—	—	9	3
MOLLUSCA	92	82	85	91	89	100	97	87
Polyplacophora	1	4	10	7	11	9	18	8
Gastropoda	52	42	43	37	44	77	74	30
Bivalvia	88	76	81	85	84	100	97	81
Scaphopoda	1	1	9	35	43	59	35	3
Cephalopoda	—	—	—	1	1	—	—	—
ARTHROPODA	88	99	100	80	71	82	53	78
Pycnogonida	2	2	2	4	—	9	3	—
Arachnida	—	—	<1	—	—	—	—	—
Crustacea	88	99	100	80	71	82	53	78
Ostracoda	—	—	<1	<1	1	5	—	3
Cirripedia	13	4	3	3	4	—	—	—
Copepoda	—	—	1	—	1	5	—	—
Cumacea	27	41	56	30	15	36	15	22
Tanaidacea	—	—	—	—	1	—	3	35
Isopoda	29	69	46	20	20	18	12	43
Amphipoda	80	95	98	72	58	77	44	54
Mysidacea	13	11	3	<1	1	—	—	—
Decapoda	37	39	35	13	4	—	3	—
BRYOZOA	19	13	11	10	12	—	—	5
BRACHIOPODA	—	—	2	10	14	5	—	—
ECHINODERMATA	39	68	71	78	84	64	65	92
Crinoidea	—	—	—	—	1	—	3	—
Holothuroidea	9	8	20	17	33	14	29	27
Echinoidea	21	57	31	16	22	—	6	16
Ophiuroidea	10	9	40	66	72	59	44	76
Asteroidea	9	9	20	16	6	5	12	5
HEMICHORDATA	—	—	1	<1	—	5	—	—
CHORDATA	14	24	19	14	12	5	15	24
Ascidiacea	14	24	19	14	12	5	15	24

Table 16
Mean number of specimens of each taxon per square meter in relation to bottom sediments.

Taxon	Bottom sediments						
	Gravel	Till	Shell	Sand	Sand-silt	Silt-clay	All types
PORIFERA	3.9	4.5	0.3	0.4	2.5	0.7	1.5
COELENTERATA	45.0	16.0	7.8	50.0	15.4	6.3	32.1
Hydrozoa	20.3	6.9	5.2	6.0	2.9	1.5	6.4
Anthozoa	24.7	10.9	2.6	44.0	12.5	4.8	25.7
Alcyonaria	1.6	—	—	0.2	0.9	1.6	0.8
Zoantharia	13.7	3.4	2.3	43.1	9.3	2.7	22.6
Unidentified	9.3	5.6	0.3	0.7	2.3	0.4	2.2
PLATYHELMINTHES	1.7	—	—	0.2	—	0.1	0.4
Turbellaria	1.7	—	—	0.2	—	0.1	0.4
NEMERTEA	4.9	0.9	27.5	13.3	5.1	3.4	8.2
ASCHELMINTHES	8.7	1.0	—	1.2	2.4	3.0	2.8
Nematoda	8.7	1.0	—	1.2	2.4	3.0	2.8
ANNELIDA	504.8	289.5	442.5	558.1	309.7	231.9	425.0
POGONOPHORA	—	—	—	<0.1	0.8	1.9	0.6
SIPUNCULIDA	4.0	4.4	6.0	7.1	5.3	5.5	5.9
ECHIURA	—	—	—	—	0.2	0.3	0.1
PRIAPULIDA	—	—	—	—	<0.1	<0.1	<0.1
MOLLUSCA	83.7	103.0	228.5	98.6	276.0	353.8	188.0
Polyplacophora	2.0	2.5	—	0.3	3.8	1.3	1.5
Gastropoda	40.3	9.1	82.7	11.2	22.0	11.9	17.8
Bivalvia	39.4	78.3	180.3	85.0	242.1	329.6	163.1
Scaphopoda	2.0	13.1	25.5	1.8	6.4	10.9	5.1
Cephalopoda	<0.1	—	—	<0.1	1.7	—	0.4
Unidentified	—	—	—	0.2	<0.1	—	0.1
ARTHROPODA	712.0	58.8	124.2	1,336.0	275.5	33.9	726.2
Pycnogonida	2.1	0.1	—	0.1	0.1	0.1	0.3
Arachnida	—	—	—	<0.1	—	—	<0.1
Crustacea	709.9	58.7	124.2	1,335.9	275.4	33.8	725.9
Ostracoda	<0.1	—	—	—	0.1	<0.1	<0.1
Cirripedia	28.7	1.0	5.0	16.4	55.5	0.2	21.8
Copepoda	—	—	—	0.1	0.1	0.1	0.1
Cumacea	10.5	1.2	7.5	45.3	18.3	7.0	25.8
Tanaidacea	—	—	—	—	0.1	0.1	<0.1
Isopoda	5.8	7.1	4.2	22.4	5.2	3.0	12.1
Amphipoda	639.7	49.5	98.8	1,237.6	193.0	23.1	655.8
Mysidacea	0.9	—	—	5.0	0.9	0.1	2.5
Decapoda	24.0	—	8.7	8.7	1.9	0.2	7.5
Unidentified	0.3	—	—	0.4	0.6	—	0.3
BRYOZOA	75.1	5.6	331.0	4.9	5.4	1.5	15.7
BRACHIOPODA	13.6	48.2	37.0	1.2	2.3	2.0	4.5
ECHINODERMATA	23.0	67.0	27.8	94.9	103.7	65.0	79.3
Crinoidea	—	—	—	—	0.1	<0.1	<0.1
Holothuroidea	3.7	25.4	2.0	2.2	7.4	4.1	4.3
Echinoidea	2.8	3.4	0.3	67.2	0.6	1.5	29.3
Ophiuroidea	15.8	38.0	25.5	23.8	94.3	57.8	44.2
Asteroidea	0.8	0.2	—	1.8	1.3	1.7	1.5
HEMICHORDATA	—	—	—	0.1	0.2	<0.1	0.1
CHORDATA	29.3	5.1	4.3	22.4	11.4	1.9	16.3
Ascidiacea	29.3	5.1	4.3	22.4	11.4	1.9	16.3
UNIDENTIFIED	2.9	5.6	—	5.8	6.4	7.0	5.8
Total	1,512.5	609.6	1,236.9	2,243.5	1,002.4	718.2	1,512.2

Table 17

The number of specimens of each taxon, expressed as a percentage of the total benthic invertebrate fauna, in relation to bottom sediments.

	Bottom sediments						
Taxon	Gravel	Till	Shell	Sand	Sand-silt	Silt-clay	All types
PORIFERA	0.3	0.7	<0.1	<0.1	0.2	0.1	0.1
COELENTERATA	3.0	2.6	0.6	2.3	1.5	0.9	2.1
Hydrozoa	1.3	1.1	0.4	0.3	0.3	0.2	0.4
Anthozoa	1.7	1.5	0.2	2.0	1.2	0.7	1.7
Alcyonaria	0.1	—	—	<0.1	0.1	0.2	0.1
Zoantharia	0.9	0.6	0.2	2.0	0.9	0.4	1.5
Unidentified	0.6	0.9	<0.1	<0.1	0.2	0.1	0.2
PLATYHELMINTHES	0.1	—	—	<0.1	—	<0.1	<0.1
Turbellaria	0.1	—	—	<0.1	—	<0.1	<0.1
NEMERTEA	0.3	0.2	2.1	0.6	0.5	0.5	0.5
ASCHELMINTHES	0.6	0.2	—	<0.1	0.2	0.4	0.2
Nematoda	0.6	0.2	—	<0.1	0.2	0.4	0.2
ANNELIDA	33.4	47.5	34.1	25.4	30.3	32.3	28.1
POGONOPHORA	—	—	—	<0.1	0.1	0.3	<0.1
SIPUNCULIDA	0.3	0.7	0.5	0.3	0.5	0.8	0.4
ECHIURA	—	—	—	—	<0.1	<0.1	<0.1
PRIAPULIDA	—	—	—	—	<0.1	<0.1	<0.1
MOLLUSCA	5.5	16.9	22.2	4.5	27.0	49.3	12.4
Polyplacophora	0.1	0.4	—	<0.1	0.4	0.2	0.1
Gastropoda	2.7	1.5	6.4	0.5	2.2	1.6	1.2
Bivalvia	2.6	12.8	13.9	3.9	23.7	45.9	10.8
Scaphopoda	0.1	2.2	2.0	0.1	0.6	1.5	0.3
Cephalopoda	<0.1	—	—	<0.1	0.2	—	<0.1
Unidentified	—	—	—	<0.1	<0.1	—	<0.1
ARTHROPODA	47.1	9.6	9.6	60.9	27.0	4.7	48.0
Pycnogonida	0.1	<0.1	—	<0.1	<0.1	<0.1	<0.1
Arachnida	—	—	—	<0.1	—	—	<0.1
Crustacea	46.9	9.6	9.6	60.9	27.0	4.7	48.0
Ostracoda	<0.1	—	—	—	<0.1	<0.1	<0.1
Cirripedia	1.9	0.2	0.4	0.8	5.4	<0.1	1.4
Copepoda	—	—	—	<0.1	<0.1	<0.1	<0.1
Cumacea	0.7	0.2	0.6	2.1	1.8	1.0	1.7
Tanaidacea	—	—	—	—	<0.1	<0.1	<0.1
Isopoda	0.4	1.2	0.3	1.0	0.5	0.4	0.8
Amphipoda	42.3	8.1	7.6	56.4	18.9	3.2	43.4
Mysidacea	0.1	—	—	0.2	0.1	<0.1	0.2
Decapoda	1.6	—	0.7	0.4	0.2	<0.1	0.5
Unidentified	<0.1	—	—	<0.1	0.1	—	<0.1
BRYOZOA	5.0	0.9	25.5	0.2	0.5	0.2	1.0
BRACHIOPODA	0.9	7.9	2.8	<0.1	0.2	0.3	0.3
ECHINODERMATA	1.5	11.0	2.2	4.3	10.2	9.0	5.2
Crinoidea	—	—	—	—	<0.1	<0.1	<0.1
Holothuroidea	0.2	4.2	0.2	0.1	0.7	0.6	0.3
Echinoidea	0.2	0.6	<0.1	3.1	0.1	0.2	1.9
Ophiuroidea	1.0	6.2	2.0	1.1	9.2	8.0	2.9
Asteroidea	<0.1	<0.1	—	0.1	0.1	0.2	0.1
HEMICHORDATA	—	—	—	<0.1	<0.1	<0.1	<0.1
CHORDATA	1.9	0.8	0.3	1.0	1.1	0.3	1.1
Ascidiacea	1.9	0.8	0.3	1.0	1.1	0.3	1.1
UNIDENTIFIED	0.2	0.9	—	0.3	0.6	1.0	0.4
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

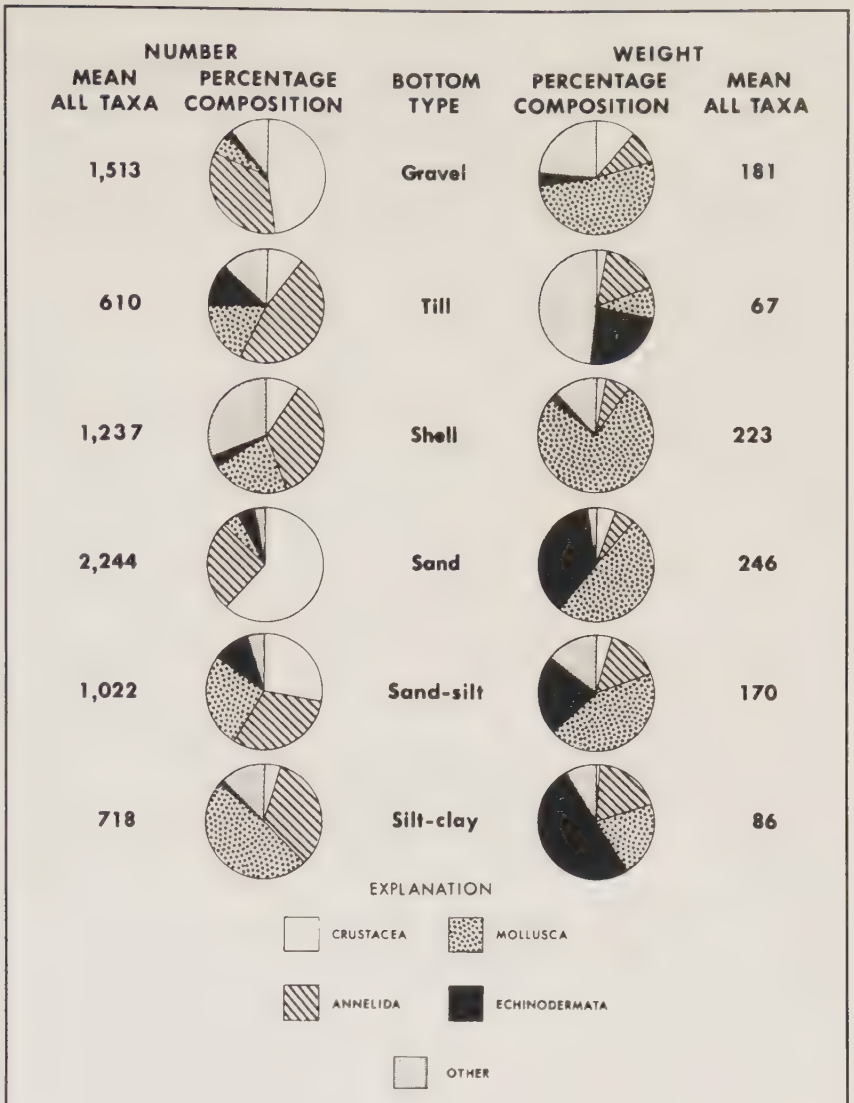


Figure 17
Quantitative composition of the total macrobenthic invertebrate fauna in relation to bottom type. Mean number of individuals and mean wet weight, per square meter of bottom area, and percentage composition, by density and biomass, of the major taxonomic groups are shown.

large part to occasional large animals. Those groups that contributed large specimens at those depths were Sipunculida, Echiura, Echinoidea, and Holothuroidea.

The percentage occurrence of each taxonomic group in samples in each depth range class is presented in Table 15.

Relation to Bottom Sediments

A marked disparity in the average density and biomass of benthic invertebrates was found among the various kinds of bottom sediments in the New England Region (Tables 16, 17; Fig. 17). Sand ranked far above the other sediment types in density, with an average of 2,244 individuals/m^2. Three sediment types—gravel, shell, and sand-silt—supported a moderate number of animals; their average densities ranged from 1,022 to 1,513/m^2. Lower densities (610 and 718/m^2) were found in till and silt-clay sediments.

Distribution of biomass (Tables 18, 19; Fig. 17) was similar to that of density. Sand and shell supported high (246 and 223 g/m^2) biomasses. Moderate quantities (170 and 181 g/m^2) occurred in gravel and sand-silt. Relatively low quantities were encountered in silt-clay and till sediments.

Table 18
Mean wet weight of specimens of each taxon (grams per square meter) in relation to bottom sediments.

Taxon	Bottom sediments						
	Gravel	Till	Shell	Sand	Sand-silt	Silt-clay	All types
PORIFERA	8.62	12.69	5.77	0.34	3.05	0.12	2.24
COELENTERATA	15.29	1.81	0.93	2.00	18.22	3.52	7.33
Hydrozoa	2.60	0.32	0.14	0.34	0.05	0.01	0.52
Anthozoa	12.69	1.49	0.79	1.66	18.17	3.51	6.81
Alcyonaria	0.09	—	—	0.22	0.29	0.20	0.20
Zoantharia	12.36	1.09	0.68	1.37	17.25	3.22	6.39
Unidentified	0.24	0.39	0.12	0.07	0.62	0.10	0.22
PLATYHELMINTHES	0.01	—	—	0.01	—	0.01	0.01
Turbellaria	0.01	—	—	0.01	—	0.01	0.01
NEMERTEA	0.52	0.06	6.09	0.81	0.83	0.46	0.71
ASCHELMINTHES	0.01	0.01	—	<0.01	0.01	0.01	0.01
Nematoda	0.01	0.01	—	<0.01	0.01	0.01	0.01
ANNELIDA	15.52	10.67	15.30	15.00	25.96	16.25	17.41
POGONOPHORA	—	—	—	<0.01	0.01	0.01	<0.01
SIPUNCULIDA	0.58	0.29	0.16	0.89	0.81	0.57	0.75
ECHIURA	—	—	—	—	0.79	0.69	0.30
PRIAPULIDA	—	—	—	—	<0.01	0.02	<0.01
MOLLUSCA	94.44	5.96	167.76	120.99	73.56	18.43	83.64
Polyplacophora	0.72	0.29	—	0.01	0.06	0.07	0.14
Gastropoda	3.25	0.21	2.13	3.32	1.60	0.22	2.23
Bivalvia	90.22	4.66	165.13	117.44	71.62	17.58	80.95
Scaphopoda	0.25	0.80	0.50	0.22	0.26	0.56	0.32
Cephalopoda	<0.01	—	—	0.01	0.02	—	0.01
Unidentified	—	—	—	<0.01	<0.01	—	<0.01
ARTHROPODA	20.32	1.93	6.26	11.92	6.95	0.62	9.41
Pycnogonida	0.05	<0.01	—	<0.01	<0.01	0.01	0.01
Arachnida	—	—	—	<0.01	—	—	<0.01
Crustacea	20.27	1.93	6.26	11.92	6.95	0.61	9.40
Ostracoda	<0.01	—	—	—	<0.01	<0.01	<0.01
Cirripedia	11.06	0.02	0.45	2.36	4.41	0.01	3.39
Copepoda	—	—	—	<0.01	<0.01	<0.01	<0.01
Cumacea	0.06	0.01	0.08	0.20	0.06	0.03	0.11
Tanaidacea	—	—	—	—	<0.01	<0.01	<0.01
Isopoda	0.21	1.36	0.04	0.44	0.14	0.09	0.29
Amphipoda	3.39	0.54	0.92	7.73	1.91	0.18	4.16
Mysidacea	0.01	—	—	0.02	0.01	<0.01	0.01
Decapoda	5.56	—	4.78	1.16	0.41	0.32	1.43
Unidentified	<0.01	—	—	<0.01	<0.01	—	<0.01
BRYOZOA	7.39	0.25	16.78	0.37	0.05	0.05	1.29
BRACHIOPODA	2.44	15.87	0.22	0.24	0.33	0.28	0.89
ECHINODERMATA	5.66	15.24	3.39	88.43	36.59	42.87	55.00
Crinoidea	—	—	—	—	<0.01	<0.01	<0.01
Holothuroidea	2.10	4.73	0.40	3.11	25.00	28.74	12.87
Echinoidea	1.98	4.73	2.25	80.68	3.43	7.26	36.75
Ophiuroidea	1.23	5.27	0.74	2.67	5.80	3.26	3.26
Asteroidea	0.34	0.50	—	1.98	2.27	3.61	2.13
HEMICHORDATA	—	—	—	0.02	0.04	<0.01	0.02
CHORDATA	9.70	1.98	0.09	4.35	2.36	1.95	4.10
Ascidiacea	9.70	1.98	0.09	4.35	2.36	1.95	4.10
UNIDENTIFIED	0.45	0.21	—	0.23	0.31	0.24	0.27
Total	180.94	66.97	222.75	245.60	169.88	86.10	183.39

Table 19

The wet weight of specimens of each taxon, expressed as a percentage of the total benthic invertebrate fauna, in relation to bottom sediments.

	Bottom sediments						
Taxon	Gravel	Till	Shell	Sand	Sand-silt	Silt-clay	All types
PORIFERA	4.8	19.0	2.6	0.1	1.8	0.1	1.2
COELENTERATA	8.5	2.7	0.4	0.8	10.7	4.1	4.0
Hydrozoa	1.4	0.5	0.1	0.1	<0.1	<0.1	0.3
Anthozoa	7.1	2.2	0.3	0.7	10.7	4.1	3.7
Alcyonaria	<0.1	—	—	0.1	0.2	0.2	0.1
Zoantharia	6.8	1.6	0.3	0.6	10.2	3.7	3.5
Unidentified	0.1	0.6	<0.1	<0.1	0.4	0.1	0.1
PLATYHELMINTHES	<0.1	—	—	<0.1	—	<0.1	<0.1
Turbellaria	<0.1	—	—	<0.1	—	<0.1	<0.1
NEMERTEA	0.3	0.1	2.7	0.3	0.5	0.5	0.4
ASCHELMINTHES	<0.1	<0.1	—	<0.1	<0.1	<0.1	<0.1
Nematoda	<0.1	<0.1	—	<0.1	<0.1	<0.1	<0.1
ANNELIDA	8.6	15.9	6.9	6.1	15.3	18.9	9.5
POGONOPHORA	—	—	—	<0.1	<0.1	<0.1	<0.1
SIPUNCULIDA	0.3	0.4	0.1	0.4	0.5	0.7	0.4
ECHIURA	—	—	—	—	0.5	0.8	0.2
PRIAPULIDA	—	—	—	—	<0.1	<0.1	<0.1
MOLLUSCA	52.2	8.9	75.3	49.3	43.3	21.4	45.6
Polyplacophora	0.4	0.4	—	<0.1	<0.1	0.1	0.1
Gastropoda	1.8	0.3	1.0	1.4	0.9	0.3	1.2
Bivalvia	49.9	7.0	74.1	47.8	42.2	20.4	44.1
Scaphopoda	0.1	1.2	0.2	0.1	0.2	0.6	0.2
Cephalopoda	<0.1	—	—	<0.1	<0.1	—	<0.1
Unidentified	—	—	—	<0.1	<0.1	—	<0.1
ARTHROPODA	11.2	2.9	2.8	4.8	4.1	0.7	5.1
Pycnogonida	<0.1	<0.1	—	<0.1	<0.1	<0.1	<0.1
Arachnida	—	—	—	<0.1	—	—	<0.1
Crustacea	11.2	2.9	2.8	4.8	4.1	0.7	5.1
Ostracoda	<0.1	—	—	—	<0.1	<0.1	<0.1
Cirripedia	6.1	<0.1	0.2	1.0	2.6	<0.1	1.8
Copepoda	—	—	—	<0.1	<0.1	<0.1	<0.1
Cumacea	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	0.1
Tanaidacea	—	—	—	—	<0.1	<0.1	<0.1
Isopoda	0.1	2.0	<0.1	0.2	0.1	0.1	0.2
Amphipoda	1.9	0.8	0.4	3.2	1.1	0.2	2.3
Mysidacea	<0.1	—	—	<0.1	<0.1	<0.1	<0.1
Decapoda	3.1	—	2.2	0.5	0.2	0.4	0.8
Unidentified	<0.1	—	—	<0.1	<0.1	—	<0.1
BRYOZOA	4.1	0.4	7.5	0.2	<0.1	0.1	0.7
BRACHIOPODA	1.4	23.7	0.1	0.1	0.2	0.3	0.5
ECHINODERMATA	3.1	22.8	1.5	36.0	21.6	49.8	30.0
Crinoidea	—	—	—	—	<0.1	<0.1	<0.1
Holothuroidea	1.2	7.1	0.2	1.3	14.8	33.4	7.0
Echinoidea	1.1	7.1	1.0	32.8	2.0	8.4	20.0
Ophiuroidea	0.7	7.9	0.3	1.1	3.4	3.8	1.8
Asteroidea	0.2	0.8	—	0.8	1.3	4.2	1.2
HEMICHORDATA	—	—	—	<0.1	<0.1	<0.1	<0.1
CHORDATA	5.4	3.0	<0.1	1.8	1.4	2.3	2.2
Ascidiacea	5.4	3.0	<0.1	1.8	1.4	2.3	2.2
UNIDENTIFIED	0.2	0.3	—	0.1	0.2	0.3	0.2
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 20
Frequency of occurrence (%) of each taxonomic group in the samples in each sediment type.

Taxon	Bottom sediments					
	Gravel	Till	Shell	Sand	Sand-silt	Silt-clay
PORIFERA	16	41	17	3	8	3
COELENTERATA	47	59	50	38	53	35
Hydrozoa	23	27	33	14	6	4
Anthozoa	24	32	17	24	47	31
Alcyonaria	4	—	—	1	10	12
Zoantharia	29	27	33	22	35	17
PLATYHELMINTHES	2	—	—	2	—	1
Turbellaria	2	—	—	2	—	1
NEMERTEA	28	14	50	42	47	29
ASCHELMINTHES	12	5	—	4	13	13
Nematoda	12	5	—	4	13	13
ANNELIDA	97	100	100	94	100	97
POGONOPHORA	—	—	—	<1	8	16
SIPUNCULIDA	20	23	17	25	28	18
ECHIURA	—	—	—	—	3	5
PRIAPULIDA	—	—	—	—	1	1
MOLLUSCA	75	96	100	86	94	93
Polyplacophora	14	27	—	3	11	9
Gastropoda	43	50	83	44	45	42
Bivalvia	68	96	100	79	92	91
Scaphopoda	17	46	33	10	30	31
Cephalopoda	1	—	—	1	1	—
ARTHROPODA	95	91	100	96	82	68
Pycnogonida	11	5	—	1	1	1
Arachnida	—	—	—	<1	—	—
Crustacea	95	91	100	96	82	68
Ostracoda	1	—	—	—	1	<1
Cirripedia	13	9	17	2	3	1
Copepoda	—	—	—	<1	1	<1
Cumacea	26	14	17	50	34	22
Tanaidacea	—	—	—	—	2	5
Isopoda	32	50	17	51	28	16
Amphipoda	93	77	100	94	74	51
Mysidacea	4	—	—	6	3	1
Decapoda	35	—	33	37	7	4
BRYOZOA	27	32	50	8	10	4
BRACHIOPODA	14	41	17	2	3	3
ECHINODERMATA	51	86	50	72	78	78
Crinoidea	—	—	—	—	1	<1
Holothuroidea	16	50	17	8	36	23
Echinoidea	14	32	17	47	8	15
Ophiuroidea	40	68	33	29	64	62
Asteroidea	8	9	—	14	16	14
HEMICHORDATA	—	—	—	<1	1	<1
CHORDATA	22	32	17	19	15	11
Ascidiacea	22	32	17	19	15	11

Figure 18

Medium coarse sand bottom at a depth of 87 m on the western Nova Scotia shelf. This locality also contains some fine angular to rounded gravel to 7 cm in size. Bivalve shell fragments litter the bottom; an intact mussel valve is visible in the upper right-center portion of the frame. The camera tripping weight is visible at upper left-center. Photograph was taken at station 1165c, located at lat. 44°09' N., long. 66°29' W.

The percentage occurrence of each taxonomic group in samples in each sediment type is presented in Table 20.

Photographs of the sea bottom (Figs. 18 to 24) taken with the photographic system in the Campbell Grab show the sediment surface and associated fauna in different bottom types in different subareas within the New England region. Sediment types range from coarse (gravels and cobbles) to fine (silty sands). The camera-tripping weight, visible in each photograph, serves as a possible indicator of the amount of silt-clay contained in the sediment depending on the quantity of material disturbed and entering into suspension upon disturbance.

Relation to Water Temperature

The abundance of the New England region macrobenthos, in general, was related directly to the annual range in water temperature. In areas with a small annual range in water temperature, the density of animals was low and the biomass small. Conversely, where the annual range in water temperature was large, the density of animals was high (Tables 21, 22; Fig. 25), and biomass large (Tables 23, 24; Fig. 25). In areas subject to annual water temperature ranges of less than 4°C, average density was only 431/m^2 and biomass only 46 g/m^2. Although there are some inconsistencies, in

Figure 19

Brown silty sand bottom at 116 m depth southwest of Grand Manan Island. A substantial number of brittlestars (Ophiuroidea) of various sizes are clearly visible, as are several burrow holes. The fine nature of the bottom at this locality is indicated by the cloud of sediment raised by the camera tripping weight striking the bottom at upper left. Photograph was taken at station 1173, located at lat. 44°28' N., long. 67°15' W.

general, density increased to 4,038/m^2 where the temperature range was greater than 20°C, and biomass rose to 467 g/m^2 where the range was 16 to 19.9°C. This close relationship of sparse fauna in stable temperature areas and rich fauna in unstable areas undergoing wide temperature fluctuations is not necessarily a direct cause-and-effect relationship of temperature alone but is the result of a combination of temperature and other environmental factors. Water masses that remain relatively constant in temperature and are unchanging in most other physical and chemical properties also tend to have more uniform biological components. In the New England region these water masses tend to be deeper, and therefore colder, darker, and lower in nutrients, plankton, nekton, as well as benthos.

The percentage occurrence of each taxonomic group in samples in each temperature range class is presented in Table 25.

Figure 20
Sand and gravel bottom at 194 m depth in the southwestern Gulf of Maine east of Cape Cod. Sediment contains some pebbles to 8 cm. Five large burrowing sea anemones (Coelenterata, Ceriantharia) are visible. Camera tripping weight is at extreme right-center. Photograph was taken at station 1052, located at lat. 42°09' N., long. 69°14' W.

Relation to Sediment Organic Carbon

Two general cause-and-effect relationships were considered in prompting the analysis of organic carbon content in the sediments. The first was the possibility of a high standing crop of benthic animals in areas of high organic carbon, due to the probability of a greater food supply in those areas; or secondly, the converse could apply, namely that areas containing large standing crops would be high in organic carbon due to biogenic activities (fecal deposits, mortality, etc.). Regardless which prevailed, high organic carbon content would be associated with high abundance.

The analysis did not reveal any clear-cut correlation between sediment organic carbon content and benthic faunal abundance. A few faunal groups exhibited good correlations, some positive and some negative, but by and large they were exceptional.

Highest average densities (Tables 26, 27; Fig. 26) of macrobenthos occurred in areas where the percentage

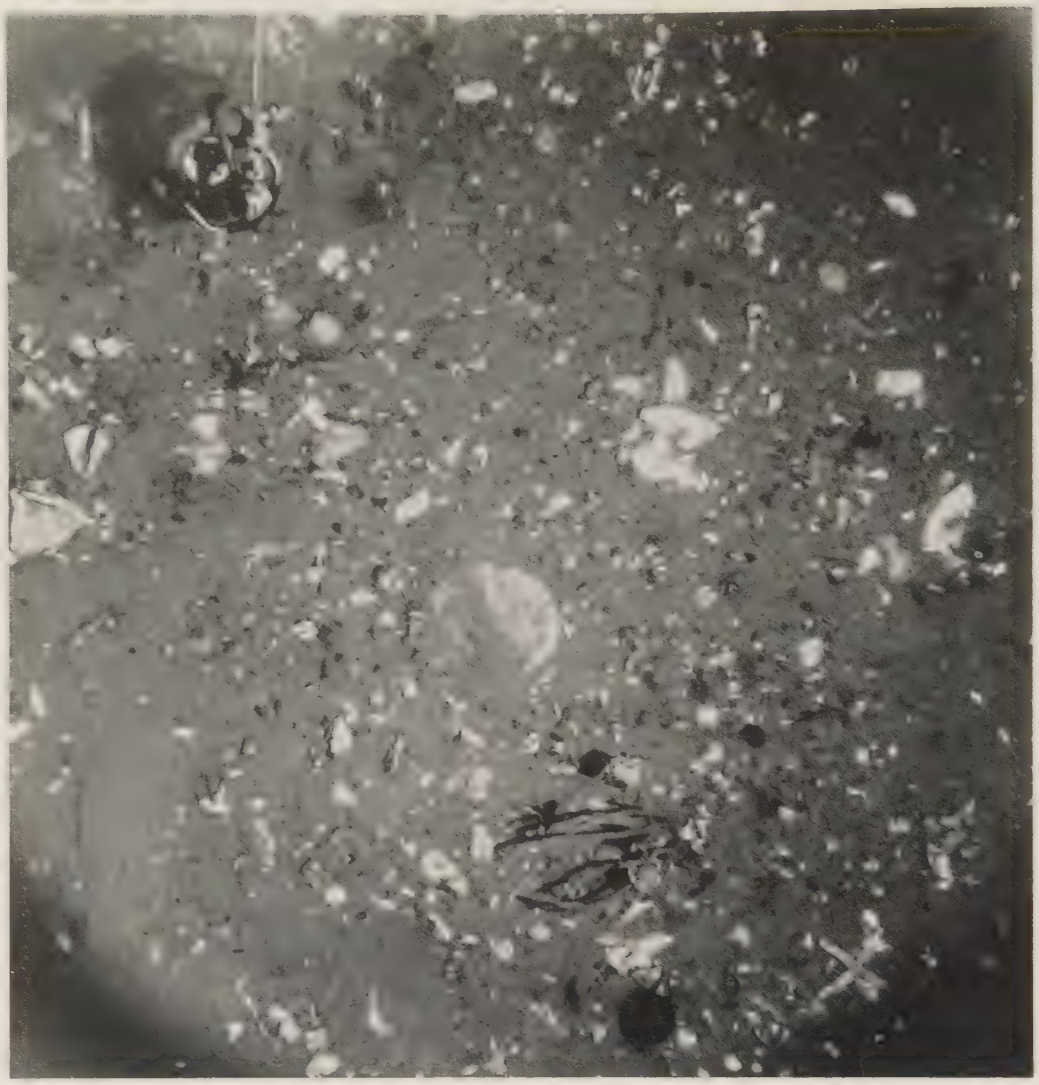


Figure 21

Medium grained brown sand and shell bottom at 88 m depth on east-central Georges Bank. Shell fraction is composed of whole and broken bivalve and gastropod shells. A large sea scallop (*Placopecten magellanicus*) valve is visible in the center of the frame; a small starfish is at lower right; a small hermit crab (Paguridae) may be seen at lower right-center on a clump of tubes. The camera trip weight is visible in the upper left corner. Photograph was taken at station 1127, located at lat. 41°30' N., long. 66°32' W.

of organic carbon in the sediments ranged from 3.0 to 4.99 (2,588/m^2) and 2.00 to 2.99 (2,042/m^2). In areas containing from 0.01 to 0.49 and from 1.00 to 1.49 percent organic carbon, densities were about 50% lower (1,858/m^2, and 1,015/m^2, respectively). Significantly lower densities occurred in other ranges; lowest densities (44/m^2) were recorded in areas containing the greatest amount of organic carbon (5% and greater). Density values over the whole range of organic carbon content as well as between adjacent classes were too variable to show any definite trends.

Correlations between the distribution of biomass and sediment organic carbon (Tables 28, 29; Fig. 26) were somewhat better but not uniform enough to denote any positive trends. Largest biomass (959 g/m^2) was recorded were organic carbon ranged between 2.00 and 2.99%, and next largest was 809 g/m^2 in the 3.00 to 4.99% range, but biomass was less than 1 g/m^2 in ranges of 5% and over.

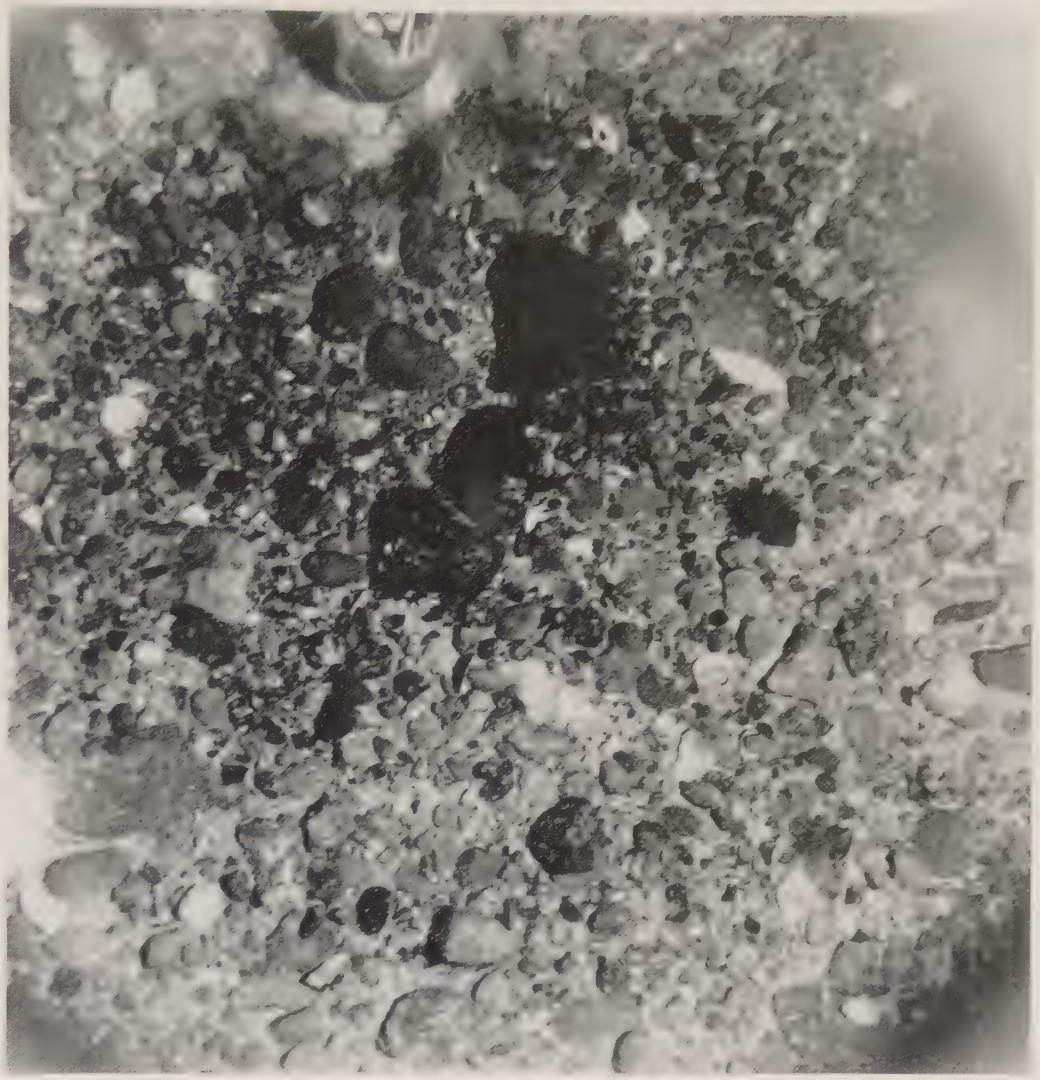


Figure 22
Coarse brown sand with broken shells and gravel, to 15 cm, bottom at 86 m depth on eastern Georges Bank. Camera tripping weight is visible at upper left-center edge of frame. Photograph was taken at station 1130, located at lat. 42°01' N., long. 66°31' W.

Biomass of 218 g/m^2 occurred in the 0.01 to 0.49% range and became rather uniform (89 to 97 g/m^2) in organic carbon contents from 0.5 to 1.99%.

The percentage occurrence of each taxonomic group in samples in each sediment organic content class is presented in Table 30.

A comparison of the similarities and differences between the macrobenthos of the New England region and that of the Middle Atlantic Bight region in relation to the environmental parameters described above is contained in Sherman et al. (1988).

Taxonomic Groups

This section deals, in turn, with each taxonomic component of the New England region macrobenthos arranged in the phylogenetic order presented in Table 4. Included for each taxon are general remarks relating to overall abundance and frequency of occurrence, as well as to aspects of the natural history of some of the common forms encountered; these remarks are followed by discussions dealing with geographic and bathymetric distribution and the quantitative relationship of

Figure 23

Medium to coarse brown sand bottom at 44 m depth on the continental shelf south of Long Island, New York. Several sand dollars (*Echinarachnius parma*) are visible; the camera tripping weight is in the upper left corner. Photograph was taken at station 1279, located at lat. 40°30' N., long. 72°30' W.

this distribution to bottom sediments, bottom water temperature, and sediment organic carbon content. This arrangement was chosen for ease of reference wherein all the information pertaining to a given taxon is presented in one place, rather than dispersed among several subsections, each dealing with a single abiotic parameter. It is our hope that this arrangement will allow the reader to make comparisons more easily among the various taxonomic groups.

Porifera

Porifera constituted a moderately small proportion of the fauna. They were generally uncommon on the continental shelf and uncommon to rare on the continental slope and rise. Specimens in our samples ranged from small (2-mm) boring species occurring on or in mollusk shells to moderately large (10 to 20 cm) *Polymastia* and *Myxilla* usually found on cobbles and boulders.

Figure 24

Green silty sand and gravel bottom at 450 m depth on the southern New England continental slope. Gravel ranged to 2 cm. The tubes of two soda straw worms (*Hyalinoecia tubicola*) are visible at left edge of the frame, and the tracks created by their movements are also visible. The silty nature of the bottom is evident by the cloud created by the camera tripping weight at right-center. Photograph taken at station 1325, located at lat. 39°20' N., long. 72°09' W.

Porifera were most common in the Nova Scotia region and along the coast of Maine. These areas have stable substrates and moderate to strong water currents.

Colorful species were rare, limited mainly to the red *Microciona*. Shades of browns and grays were the most common colors. The colorless Hexactinellida (glass sponges) occurred only in deep water, greater than 500 m.

Porifera occurred in 71 samples (7% of total); density averaged 1.5/m^2 and biomass averaged 2.2 g/m^2 (Table 5).

Geographic Distribution

Porifera were clearly more abundant off Nova Scotia and in the Gulf of Maine than to the south and west (Fig. 27). They were common along the western coast of Nova Scotia, particularly in the mouth of the Bay of Fundy, along the Maine coast, and in the eastern Gulf of Maine. The scarcity of sponges on the continental shelf between central Georges Bank and New Jersey was especially noteworthy.

Table 21

Mean number of specimens of each taxon per square meter in relation to the annual range in bottom water temperature.

Taxon	Annual range in water temperature (degrees Celsius)						
	0–3.9	4–7.9	8–11.9	12–15.9	16–19.9	20–23.9	All ranges
PORIFERA	1.1	1.7	1.1	2.7	1.9	0.4	1.5
COELENTERATA	6.6	14.7	24.0	105.3	44.8	93.9	32.1
Hydrozoa	0.9	5.0	4.5	4.5	36.8	45.9	6.4
Anthozoa	5.7	9.7	19.5	100.8	8.0	48.0	25.7
Alcyonaria	1.1	1.2	0.2	1.7	—	—	0.8
Zoantharia	2.4	7.9	18.6	98.4	7.2	4.4	22.6
Unidentified	2.1	0.6	0.7	0.7	0.8	43.6	2.2
PLATYHELMINTHES	—	0.2	1.0	0.1	<0.1	0.4	0.4
Turbellaria	—	0.2	1.0	0.1	<0.1	0.4	0.4
NEMERTEA	2.4	4.2	9.0	25.3	4.4	2.9	8.2
ASCHELMINTHES	3.5	2.0	4.3	0.7	0.2	—	2.8
Nematoda	3.5	2.0	4.3	0.7	0.2	—	2.8
ANNELIDA	211.5	513.2	568.2	279.8	370.4	1,697.8	425.0
POGONOPHORA	1.5	0.7	0.1	—	—	—	0.6
SIPUNCULIDA	4.5	9.0	8.5	2.8	2.6	—	5.9
ECHIURA	0.1	0.3	—	—	0.4	—	0.1
PRIAPULIDA	<0.1	—	—	—	—	—	<0.1
MOLLUSCA	84.0	129.2	129.2	344.9	344.5	1,242.2	188.0
Polyplacophora	1.4	0.8	0.8	2.0	7.3	—	1.5
Gastropoda	9.4	15.1	14.8	13.1	84.9	47.4	17.8
Bivalvia	64.4	102.9	110.1	329.0	252.0	1,194.8	163.1
Scaphopoda	8.9	10.3	2.1	0.8	0.2	—	5.1
Cephalopoda	<0.1	0.1	1.1	—	—	—	0.4
Unidentified	<0.1	—	0.3	—	—	—	0.1
ARTHROPODA	64.9	338.0	1,475.6	768.3	1,040.1	903.5	726.2
Pycnogonida	0.1	0.4	0.7	0.1	0.2	1.5	0.3
Arachnida	—	<0.1	—	—	—	—	<0.1
Crustacea	64.8	337.6	1,474.9	768.2	1,039.9	902.0	725.9
Ostracoda	0.1	<0.1	—	—	—	—	<0.1
Cirripedia	0.3	8.7	14.2	14.0	154.4	196.1	21.8
Copepoda	0.1	—	—	0.1	—	—	<0.1
Cumacea	2.3	9.6	56.3	21.3	43.5	19.0	25.8
Tanaidacea	0.1	0.1	—	—	—	—	<0.1
Isopoda	2.6	3.8	15.7	25.1	7.0	67.3	12.1
Amphipoda	58.2	311.6	1,371.9	694.7	808.5	598.2	655.8
Mysidacea	<0.1	0.8	3.4	6.3	3.4	6.1	2.5
Decapoda	0.9	3.2	13.2	6.4	23.2	13.4	7.5
Unidentified	0.5	—	0.2	0.4	—	1.9	0.3
BRYOZOA	3.0	9.5	15.8	35.1	28.3	66.0	15.7
BRACHIOPODA	8.5	5.9	3.0	—	—	—	4.5
ECHINODERMATA	32.9	61.5	104.7	171.2	31.5	21.0	79.3
Crinoidea	<0.1	—	—	—	—	—	<0.1
Holothuroidea	6.3	4.1	3.7	2.8	1.7	3.5	4.3
Echinoidea	1.4	4.9	40.4	93.1	26.8	14.6	29.3
Ophiuroidea	24.8	50.4	57.9	74.1	2.0	2.4	44.2
Asteroidea	0.4	2.2	2.7	1.2	0.9	0.5	1.5
HEMICHORDATA	<0.1	—	0.2	0.2	—	—	0.1
CHORDATA	2.0	2.3	35.1	6.0	58.5	4.3	16.3
Ascidiacea	2.0	2.3	35.1	6.0	58.5	4.3	16.3
UNIDENTIFIED	5.6	5.7	6.6	4.2	6.6	5.2	5.8
Total	432.2	1,097.9	2,386.2	1,746.4	1,934.2	4,037.5	1,512.2

Table 22

The number of specimens of each taxon, expressed as a percentage of the total benthic invertebrate fauna, in relation to the annual range in bottom water temperature.

	Annual range in water temperature (degrees Celsius)						
Taxon	0–3.9	4–7.9	8–11.9	12–15.9	16–19.9	20–23.9	All ranges
PORIFERA	0.3	0.2	<0.1	0.2	0.1	<0.1	0.1
COELENTERATA	1.5	1.3	1.0	6.0	2.3	2.3	2.1
Hydrozoa	0.2	0.4	0.2	0.3	1.9	1.1	0.4
Anthozoa	1.3	0.9	0.8	5.7	0.4	1.2	1.7
Alcyonaria	0.3	0.1	<0.1	0.1	—	—	0.1
Zoantharia	0.6	0.7	0.8	5.6	0.4	0.1	1.5
Unidentified	0.5	0.1	<0.1	<0.1	<0.1	1.1	0.2
PLATYHELMINTHES	—	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Turbellaria	—	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
NEMERTEA	0.6	0.4	0.4	1.4	0.2	0.1	0.5
ASCHELMINTHES	0.8	0.2	0.2	<0.1	<0.1	—	0.2
Nematoda	0.8	0.2	0.2	<0.1	<0.1	—	0.2
ANNELIDA	48.9	46.7	23.8	16.0	19.2	42.0	28.1
POGONOPHORA	0.3	0.1	<0.1	—	—	—	<0.1
SIPUNCULIDA	1.0	0.8	0.4	0.2	0.1	—	0.4
ECHIURA	<0.1	<0.1	—	—	<0.1	—	<0.1
PRIAPULIDA	<0.1	—	—	—	—	—	<0.1
MOLLUSCA	19.4	11.8	5.4	19.8	17.8	30.8	12.4
Polyplacophora	0.3	0.1	<0.1	0.1	0.4	—	0.1
Gastropoda	2.2	1.4	0.6	0.8	4.4	1.2	1.2
Bivalvia	14.9	9.4	4.6	18.8	13.0	29.6	10.8
Scaphopoda	2.0	0.9	0.1	<0.1	<0.1	—	0.3
Cephalopoda	<0.1	<0.1	<0.1	—	—	—	<0.1
Unidentified	<0.1	—	<0.1	—	—	—	<0.1
ARTHROPODA	15.0	30.8	61.8	44.0	53.8	22.4	48.0
Pycnogonida	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Arachnida	—	<0.1	—	—	—	—	<0.1
Crustacea	15.0	30.8	61.8	44.0	53.8	22.3	48.0
Ostracoda	<0.1	<0.1	—	—	—	—	<0.1
Cirripedia	0.1	0.8	0.6	0.8	8.0	4.9	1.4
Copepoda	<0.1	—	—	<0.1	—	—	<0.1
Cumacea	0.5	0.9	2.4	1.2	2.2	0.5	1.7
Tanaidacea	<0.1	<0.1	—	—	—	—	<0.1
Isopoda	0.6	0.3	0.7	1.4	0.4	1.7	0.8
Amphipoda	13.5	28.4	57.5	39.8	41.8	14.8	43.4
Mysidacea	0.1	0.1	0.1	0.4	0.2	0.2	0.2
Decapoda	0.2	0.3	0.6	0.4	1.2	0.3	0.5
Unidentified	0.1	—	<0.1	<0.1	—	<0.1	<0.1
BRYOZOA	0.7	0.9	0.7	2.0	1.5	1.6	1.0
BRACHIOPODA	2.0	0.5	0.1	—	—	—	0.3
ECHINODERMATA	7.6	5.6	4.4	9.8	1.6	0.5	5.2
Crinoidea	<0.1	—	—	—	—	—	<0.1
Holothuroidea	1.5	0.4	0.2	0.2	0.1	0.1	0.3
Echinoidea	0.3	0.4	1.7	5.3	0.6	0.4	1.9
Ophiuroidea	5.8	4.6	2.4	4.2	0.1	0.1	2.9
Asteroidea	0.1	0.2	0.1	0.1	<0.1	<0.1	0.1
HEMICHORDATA	<0.1	—	<0.1	<0.1	—	—	<0.1
CHORDATA	0.5	0.2	1.5	0.3	3.0	0.1	1.1
Ascidiacea	0.5	0.2	1.5	0.3	3.0	0.1	1.1
UNIDENTIFIED	1.3	0.5	0.3	0.2	0.3	0.1	0.4
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 23

Mean wet weight of specimens of each taxon (grams per square meter) in relation to the annual range in bottom water temperature.

Taxon	Annual range in water temperature (degrees Celsius)						
	0–3.9	4–7.9	8–11.9	12–15.9	16–19.9	20–23.9	All ranges
PORIFERA	0.86	2.50	4.65	1.08	0.10	<0.01	2.24
COELENTERATA	9.10	6.74	8.74	2.85	5.15	2.47	7.88
Hydrozoa	0.01	2.02	0.15	0.45	1.34	0.68	0.52
Anthozoa	9.09	4.72	8.59	2.40	3.61	1.79	6.81
Alcyonaria	0.42	0.11	0.04	0.81	—	—	0.20
Zoantharia	8.17	4.59	8.49	2.00	3.57	0.86	6.39
Unidentified	0.48	0.02	0.07	0.49	0.05	0.93	0.22
PLATYHELMINTHES	—	0.01	0.01	<0.01	<0.01	0.09	0.01
Turbellaria	—	0.01	0.01	<0.01	<0.01	0.09	0.01
NEMERTEA	1.22	0.53	0.89	1.22	1.38	1.11	0.71
ASCHELMINTHES	0.01	0.01	0.01	0.01	<0.01	—	0.01
Nematoda	0.01	0.01	0.01	0.01	<0.01	—	0.01
ANNELIDA	9.69	14.75	24.31	15.89	28.48	36.74	17.41
POGONOPHORA	0.01	<0.01	<0.01	—	—	—	<0.01
SIPUNCULIDA	0.73	1.01	0.97	0.54	0.33	—	0.75
ECHIURA	0.89	0.02	—	—	0.39	—	0.39
PRIAPULIDA	0.01	—	—	—	—	—	<0.01
MOLLUSCA	7.57	22.13	128.88	109.06	348.39	87.55	88.64
Polyplacophora	0.12	0.09	0.01	0.04	1.53	—	0.14
Gastropoda	0.26	1.82	8.75	2.67	4.96	4.09	2.28
Bivalvia	6.76	19.79	124.94	106.26	334.10	83.46	85.95
Scaphopoda	0.43	0.92	0.11	0.08	<0.01	—	0.32
Cephalopoda	<0.01	0.02	0.02	—	—	—	<0.01
Unidentified	<0.01	—	<0.01	—	—	—	<0.01
ARTHROPODA	1.22	3.42	16.45	12.52	16.04	24.65	9.41
Pycnogonida	<0.01	0.03	0.01	<0.01	<0.01	0.01	0.01
Arachnida	—	<0.01	—	—	—	—	<0.01
Crustacea	1.22	3.39	16.44	12.52	16.04	24.64	9.40
Ostracoda	<0.01	<0.01	—	—	—	—	<0.01
Cirripedia	0.05	0.22	6.39	3.52	3.32	20.32	3.39
Copepoda	<0.01	—	—	<0.01	—	—	<0.01
Cumacea	0.02	0.04	0.26	0.07	0.18	0.06	0.11
Tanaidacea	<0.01	<0.01	—	—	—	—	<0.01
Isopoda	0.27	0.08	0.42	0.54	0.07	0.41	0.29
Amphipoda	0.41	2.02	8.12	5.81	6.27	2.86	4.16
Mysidacea	<0.01	<0.01	0.02	0.02	0.03	0.02	0.01
Decapoda	0.47	1.02	1.28	3.24	4.26	1.25	1.48
Unidentified	<0.01	—	<0.01	<0.01	—	0.02	<0.01
BRYOZOA	0.28	0.56	2.10	2.43	0.87	2.43	1.29
BRACHIOPODA	1.93	0.75	0.57	—	—	—	0.89
ECHINODERMATA	12.24	31.85	55.48	172.85	59.63	268.42	55.86
Crinoidea	<0.01	—	—	—	—	—	<0.01
Holothuroidea	3.10	7.77	11.75	18.66	38.13	127.96	12.87
Echinoidea	6.86	14.29	17.68	148.06	37.65	134.46	36.75
Ophiuroidea	3.05	5.82	3.28	2.77	0.22	0.53	3.26
Asteroidea	3.09	3.48	2.82	3.33	3.61	0.46	2.13
HEMICHORDATA	<0.01	—	0.04	0.03	—	—	0.02
CHORDATA	0.55	4.14	7.28	1.43	14.40	0.56	4.10
Ascidiacea	0.55	4.14	7.28	1.43	14.40	0.56	4.10
UNIDENTIFIED	0.16	0.22	0.36	0.42	0.26	0.09	0.27
Total	45.48	88.11	230.67	317.62	467.42	422.12	183.89

Table 24

The wet weight of specimens of each taxon, expressed as a percentage of the total benthic invertebrate fauna, in relation to the annual range in bottom water temperature.

	Annual range in water temperature (degrees Celsius)						
Taxon	0–3.9	4–7.9	8–11.9	12–15.9	16–19.9	20–23.9	All ranges
PORIFERA	1.9	2.8	2.0	0.3	<0.1	<0.1	1.2
COELENTERATA	20.0	7.6	3.8	0.9	1.1	0.6	4.0
Hydrozoa	<0.1	2.3	0.1	0.1	0.3	0.2	0.3
Anthozoa	20.0	5.3	3.7	0.8	0.8	0.4	3.7
Alcyonaria	0.9	0.1	<0.1	0.1	—	—	0.1
Zoantharia	18.0	5.2	3.7	0.6	0.8	0.2	3.5
Unidentified	1.1	<0.1	<0.1	<0.1	<0.1	0.2	0.1
PLATYHELMINTHES	—	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Turbellaria	—	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
NEMERTEA	0.5	0.6	0.4	0.4	0.3	0.3	0.4
ASCHELMINTHES	<0.1	<0.1	<0.1	<0.1	<0.1	—	<0.1
Nematoda	<0.1	<0.1	<0.1	<0.1	<0.1	—	<0.1
ANNELIDA	21.3	16.8	10.5	4.2	6.1	9.4	9.5
POGONOPHORA	<0.1	<0.1	<0.1	—	—	—	<0.1
SIPUNCULIDA	1.6	1.2	0.4	0.1	0.1	—	0.4
ECHIURA	2.0	<0.1	—	—	0.1	—	0.2
PRIAPULIDA	<0.1	—	—	—	—	—	<0.1
MOLLUSCA	16.6	25.1	55.8	34.3	72.8	20.7	45.6
Polyplacophora	0.3	0.1	<0.1	<0.1	0.3	—	0.1
Gastropoda	0.6	1.5	1.6	0.8	1.1	1.0	1.2
Bivalvia	14.9	22.5	54.2	33.4	71.5	19.8	44.1
Scaphopoda	1.0	1.0	<0.1	<0.1	<0.1	—	0.2
Cephalopoda	<0.1	<0.1	<0.1	—	—	—	<0.1
Unidentified	<0.1	—	<0.1	—	—	—	<0.1
ARTHROPODA	2.7	3.9	7.1	3.9	3.4	5.8	5.1
Pycnogonida	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Arachnida	—	<0.1	—	—	—	—	<0.1
Crustacea	2.7	3.8	7.1	3.9	3.4	5.8	5.1
Ostracoda	<0.1	<0.1	—	—	—	—	<0.1
Cirripedia	0.1	0.2	2.8	1.1	1.1	4.8	1.8
Copepoda	<0.1	—	—	<0.1	—	—	<0.1
Cumacea	<0.1	<0.1	0.1	<0.1	<0.1	<0.1	0.1
Tanaidacea	<0.1	<0.1	—	—	—	—	<0.1
Isopoda	0.6	0.1	0.2	0.1	<0.1	0.1	0.2
Amphipoda	0.9	2.3	3.5	1.7	1.3	0.6	2.3
Mysidacea	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Decapoda	1.0	1.2	0.5	1.0	0.9	0.3	0.8
Unidentified	<0.1	—	<0.1	<0.1	—	<0.1	<0.1
BRYOZOA	0.6	0.6	0.9	0.8	0.2	0.6	0.7
BRACHIOPODA	4.2	0.8	0.2	—	—	—	0.5
ECHINODERMATA	26.9	35.6	15.4	54.4	12.8	62.4	30.0
Crinoidea	<0.1	—	—	—	—	—	<0.1
Holothuroidea	6.8	8.8	5.1	5.9	3.9	30.3	7.0
Echinoidea	13.2	16.2	7.6	46.6	8.1	31.8	20.0
Ophiuroidea	6.7	6.6	1.4	0.9	<0.1	0.1	1.8
Asteroidea	0.2	4.0	1.2	1.0	0.8	0.1	1.2
HEMICHORDATA	<0.1	—	<0.1	<0.1	—	—	<0.1
CHORDATA	1.2	4.7	3.2	0.4	3.1	0.1	2.2
Ascidiacea	1.2	4.7	3.2	0.4	3.1	0.1	2.2
UNIDENTIFIED	0.4	0.2	0.2	0.1	0.1	<0.1	0.2
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

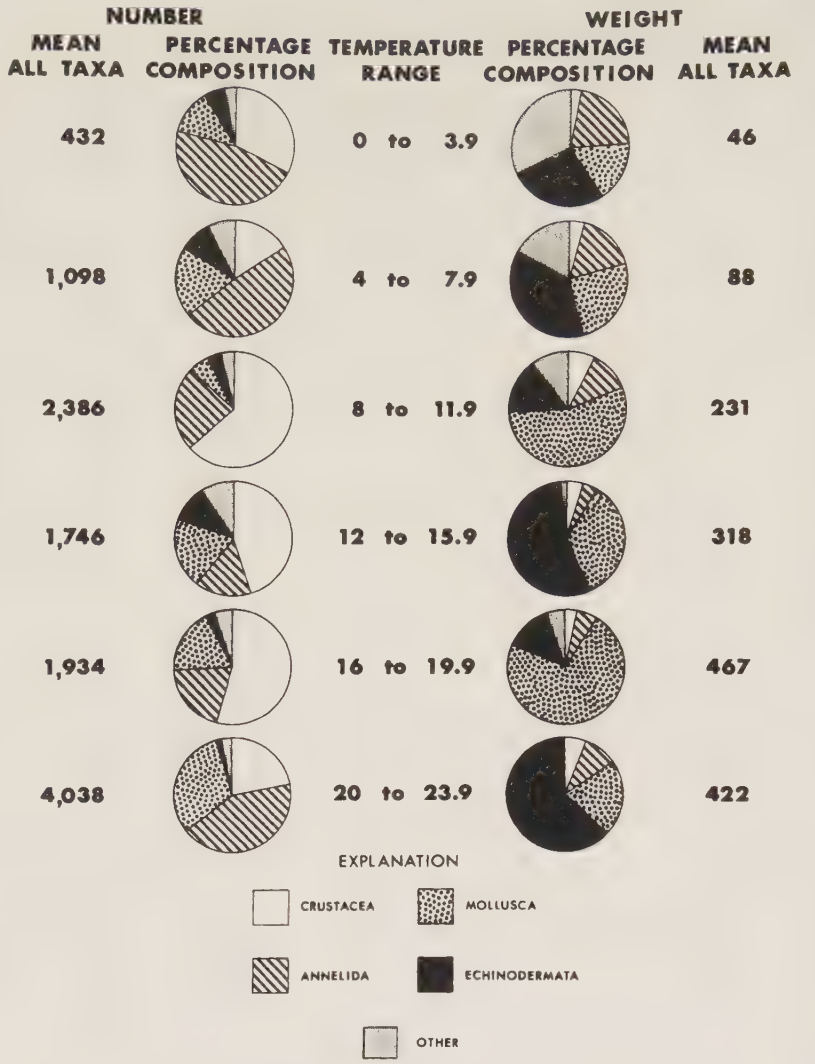


Figure 25

Quantitative composition of the total macrobenthic invertebrate fauna in relation to the annual range in bottom water temperature. Mean number of individuals and mean wet weight, per square meter of bottom area, and percentage composition, by density and biomass, for the major taxonomic groups are shown.

A pronounced decrease in abundance of sponges in each geographic region from Nova Scotia southwestward to Southern New England was evident in weight, number, and frequency of occurrence (Tables 5–10; Fig. 28). Porifera were particularly scarce in the Southern New England subarea.

Bathymetric Distribution

Porifera were moderately common to scarce on the continental shelf and upper continental slope (to 500 m), 1 to 3 individuals/m^2, and were very scarce (<0.4/m^2) at depths >500 m (Table 11; Fig. 29). Biomass also was moderate on the continental shelf and upper slope and small on the middle and lower slope and continen-

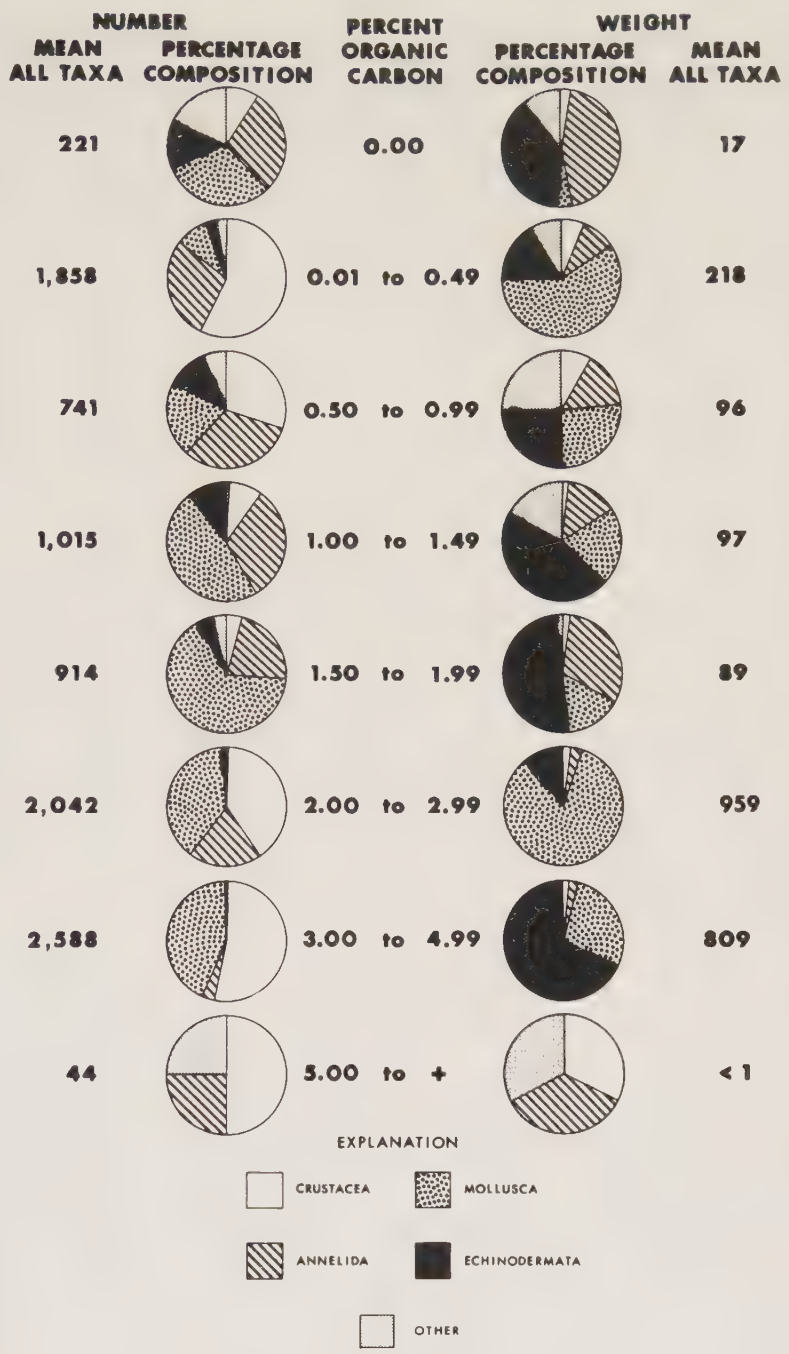


Figure 26

Quantitative composition of the total macrobenthic invertebrate fauna in relation to organic carbon in the sediments. Mean number of individuals and mean wet weight, per square meter of bottom, and percentage composition, by density and biomass, for the major taxonomic groups are shown.

tal rise (Table 13; Fig. 29). In the various depth classes average biomass ranged from 0.02 to 3.1 g/m^2. In deeper water the average weights were only 0.02 to 0.6 g/m^2.

In all depths Porifera accounted for a small percentage (<1%) of the total number of benthic animals (Table 12). The percentage of the total weight of the

Table 25
Frequency of occurrence (%) of each taxonomic group in the samples in each temperature range class.

Taxon	Annual range in water temperature (degrees Celsius)					
	0–3.9	4–7.9	8–11.9	12–15.9	16–19.9	20–23.9
PORIFERA	8	15	4	2	8	4
COELENTERATA	36	42	45	45	49	29
Hydrozoa	4	13	15	14	26	18
Anthozoa	32	29	30	31	23	11
Alcyonaria	11	5	2	8	—	—
Zoantharia	17	29	30	28	24	14
PLATYHELMINTHES	—	1	3	1	2	4
Turbellaria	—	1	3	1	2	4
NEMERTEA	25	28	49	50	52	11
ASCHELMINTHES	17	6	7	5	2	—
Nematoda	17	6	7	5	2	—
ANNELIDA	97	95	97	92	97	96
POGONOPHORA	15	3	<1	—	—	—
SIPUNCULIDA	25	29	29	12	5	—
ECHIURA	4	1	—	—	3	—
PRIAPULIDA	1	—	—	—	—	—
MOLLUSCA	91	83	87	87	94	93
Polyplacophora	10	10	6	7	5	—
Gastropoda	44	46	44	38	57	43
Bivalvia	87	75	81	83	90	93
Scaphopoda	36	37	10	3	2	—
Cephalopoda	<1	2	<1	—	—	—
ARTHROPODA	70	89	98	98	90	86
Pycnogonida	1	4	3	1	2	4
Arachnida	—	1	—	—	—	—
Crustacea	70	89	98	98	90	86
Ostracoda	1	1	—	—	—	—
Cirripedia	2	4	4	4	5	18
Copepoda	1	—	—	1	—	—
Cumacea	19	37	54	38	31	36
Tanaidacea	4	1	—	—	—	—
Isopoda	20	27	46	61	31	43
Amphipoda	57	83	97	92	82	71
Mysidacea	<1	2	3	9	13	18
Decapoda	6	15	35	31	53	18
BRYOZOA	8	13	11	11	21	18
BRACHIOPODA	10	8	2	—	—	—
ECHINODERMATA	77	78	72	71	45	43
Crinoidea	1	—	—	—	—	—
Holothuroidea	25	20	14	18	8	21
Echinoidea	16	26	33	44	24	14
Ophiuroidea	64	62	35	29	15	11
Asteroidea	6	16	21	12	11	4
HEMICHORDATA	<1	—	1	1	—	—
CHORDATA	12	11	24	17	19	11
Ascidiacea	12	11	24	17	19	11

Table 26
Mean number of specimens of each taxon per square meter in relation to sediment organic carbon content.

Taxon	Sediment organic carbon content (percent)								
	0.00	0.01–0.49	0.50–0.99	1.00–1.49	1.50–1.99	2.00–2.99	3.00–4.99	5.00+	All ranges
PORIFERA	2.6	2.7	0.5	0.4	0.2	—	—	—	1.7
COELENTERATA	—	17.8	26.8	10.1	5.3	5.3	—	—	17.7
Hydrozoa	—	8.7	9.2	3.4	0.6	2.5	—	—	7.5
Anthozoa	—	9.1	17.6	6.7	4.7	2.8	—	—	10.2
Alcyonaria	—	0.6	1.2	0.4	—	—	—	—	0.6
Zoantharia	—	7.4	6.8	4.4	4.6	2.8	—	—	6.6
Unidentified	—	1.1	9.6	1.9	0.1	—	—	—	3.0
PLATYHELMINTHES	—	0.6	0.1	—	—	0.9	—	—	0.4
Turbellaria	—	0.6	0.1	—	—	0.9	—	—	0.4
NEMERTEA	10.8	5.5	4.4	4.4	3.5	1.7	—	—	4.9
ASCHELMINTHES	—	3.1	1.0	2.8	0.4	—	—	—	2.3
Nematoda	—	3.1	1.0	2.8	0.4	—	—	—	2.3
ANNELIDA	64.0	503.6	234.7	319.1	195.9	406.9	81.3	11.0	395.7
POGONOPHORA	—	0.2	2.2	1.2	0.1	—	—	—	0.8
SIPUNCULIDA	2.2	6.9	7.3	1.0	0.1	—	—	—	5.7
ECHIURA	—	<0.1	0.3	0.1	—	—	—	—	0.1
PRIAPULIDA	—	<0.1	<0.1	0.1	—	—	—	—	<0.1
MOLLUSCA	68.8	139.1	146.7	481.7	602.1	794.7	1,119.5	—	223.3
Polyplacophora	—	2.5	0.7	1.2	0.1	—	—	—	1.7
Gastropoda	2.4	20.1	12.6	25.7	44.9	39.4	—	—	20.6
Bivalvia	64.2	113.7	125.6	442.3	545.2	750.7	1,119.5	—	195.5
Scaphopoda	2.2	2.7	5.7	12.5	11.9	4.6	—	—	5.0
Cephalopoda	—	0.1	2.1	—	—	—	—	—	0.5
Unidentified	—	—	<0.1	—	—	—	—	—	<0.1
ARTHROPODA	21.0	1,066.3	220.3	86.0	34.4	818.3	1,357.1	22.0	690.4
Pycnogonida	—	0.4	0.3	0.1	—	—	—	—	0.3
Arachnida	—	<0.1	—	—	—	—	—	—	<0.1
Crustacea	21.0	1,065.9	220.0	85.9	34.4	818.3	1,357.1	22.0	690.1
Ostracoda	—	<0.1	0.1	—	—	—	—	—	<0.1
Cirripedia	—	19.1	39.3	—	—	612.8	83.8	—	31.1
Copepoda	—	<0.1	<0.1	0.1	—	—	—	—	<0.1
Cumacea	2.6	25.2	6.1	3.8	6.2	122.8	—	—	18.7
Tanaidacea	—	<0.1	0.2	—	—	—	—	—	0.1
Isopoda	8.6	13.3	5.0	3.5	0.8	7.9	17.8	—	9.4
Amphipoda	9.8	1,000.1	164.1	78.0	24.4	66.0	1,255.5	22.0	624.4
Mysidacea	—	1.6	0.8	—	1.8	0.9	—	—	1.2
Decapoda	—	6.4	3.4	0.5	1.2	7.9	—	—	4.7
Unidentified	—	0.2	1.0	—	—	—	—	—	0.3
BRYOZOA	7.8	21.4	1.2	1.7	35.1	—	26.5	—	14.9
BRACHIOPODA	16.0	5.6	5.1	2.8	—	—	—	—	4.7
ECHINODERMATA	28.0	57.8	79.6	90.5	33.5	6.6	3.3	—	63.6
Crinoidea	—	<0.1	<0.1	—	—	—	—	—	<0.1
Holothuroidea	18.2	4.2	6.1	7.7	2.2	1.7	3.3	—	4.9
Echinoidea	2.6	23.8	0.8	0.6	1.0	—	—	—	13.8
Ophiuroidea	7.2	28.7	71.7	80.6	29.9	4.9	—	—	43.7
Asteroidea	—	1.1	1.0	1.6	0.4	—	—	—	1.0
HEMICHORDATA	—	0.2	0.2	0.1	—	—	—	—	0.1
CHORDATA	—	21.3	3.8	6.4	—	4.4	—	—	13.8
Ascidiacea	—	21.3	3.8	6.4	—	4.4	—	—	13.8
UNIDENTIFIED	—	6.3	6.6	6.8	3.1	3.0	—	11.0	6.1
Total	221.2	1,858.4	740.7	1,015.2	913.8	2,041.5	2,587.5	44.0	1,446.3

Table 27

The number of specimens of each taxon, expressed as a percentage of the total benthic invertebrate fauna, in relation to sediment organic carbon content.

	Sediment organic carbon content (percent)								
Taxon	0.00	0.01–0.49	0.50–0.99	1.00–1.49	1.50–1.99	2.00–2.99	3.00–4.99	5.00+	All ranges
PORIFERA	1.2	0.1	0.1	<0.1	<0.1	—	—	—	0.1
COELENTERATA	—	1.0	3.6	1.0	0.6	0.3	—	—	1.2
Hydrozoa	—	0.5	1.2	0.3	0.1	0.1	—	—	0.5
Anthozoa	—	0.5	2.4	0.7	0.5	0.1	—	—	0.7
Alcyonaria	—	<0.1	0.2	<0.1	—	—	—	—	<0.1
Zoantharia	—	0.4	0.9	0.4	0.5	0.1	—	—	0.5
Unidentified	—	0.1	1.3	0.2	<0.1	—	—	—	0.2
PLATYHELMINTHES	—	<0.1	<0.1	—	—	<0.1	—	—	<0.1
Turbellaria	—	<0.1	<0.1	—	—	<0.1	—	—	<0.1
NEMERTEA	4.9	0.3	0.6	0.4	0.4	0.1	—	—	0.3
ASCHELMINTHES	—	0.2	0.1	0.3	0.1	—	—	—	0.2
Nematoda	—	0.2	0.1	0.3	0.1	—	—	—	0.2
ANNELIDA	28.9	27.1	31.7	31.4	21.4	19.9	3.1	25.0	27.4
POGONOPHORA	—	<0.1	0.3	0.1	<0.1	—	—	—	0.1
SIPUNCULIDA	1.0	0.4	1.0	0.1	<0.1	—	—	—	0.4
ECHIURA	—	<0.1	<0.1	<0.1	—	—	—	—	<0.1
PRIAPULIDA	—	<0.1	<0.1	<0.1	—	—	—	—	<0.1
MOLLUSCA	31.1	7.5	19.8	47.5	65.9	38.9	43.3	—	15.4
Polyplacophora	—	0.1	0.1	0.1	<0.1	—	—	—	0.1
Gastropoda	1.1	1.1	1.7	2.5	4.9	1.9	—	—	1.4
Bivalvia	29.0	6.1	17.0	43.6	59.7	36.8	43.3	—	13.5
Scaphopoda	1.0	0.2	0.8	1.2	1.3	0.2	—	—	0.4
Cephalopoda	—	<0.1	0.3	—	—	—	—	—	<0.1
Unidentified	—	<0.1	—	—	—	—	—	—	<0.1
ARTHROPODA	9.5	57.4	29.8	8.5	3.8	40.1	52.5	50.0	47.8
Pycnogonida	—	<0.1	0.1	<0.1	—	—	—	—	<0.1
Arachnida	—	<0.1	—	—	—	—	—	—	<0.1
Crustacea	9.5	57.4	29.7	8.5	3.8	40.1	52.5	50.0	47.8
Ostracoda	—	<0.1	<0.1	—	—	—	—	—	<0.1
Cirripedia	—	1.0	5.3	—	—	30.0	3.3	—	2.2
Copepoda	—	<0.1	<0.1	<0.1	—	—	—	—	<0.1
Cumacea	1.2	1.4	0.8	0.4	0.7	6.0	—	—	1.3
Tanaidacea	—	<0.1	<0.1	—	—	—	—	—	<0.1
Isopoda	3.9	0.7	0.7	0.3	0.1	0.4	0.7	—	0.7
Amphipoda	4.4	53.8	22.2	7.7	2.7	3.2	48.5	50.0	43.2
Mysidacea	—	0.1	0.1	—	0.2	<0.1	—	—	0.1
Decapoda	—	0.3	0.5	0.1	0.1	0.4	—	—	0.3
Unidentified	—	<0.1	0.1	—	—	—	—	—	<0.1
BRYOZOA	3.5	1.1	0.2	0.2	3.9	—	1.0	—	1.0
BRACHIOPODA	7.2	0.3	0.7	0.3	—	—	—	—	0.3
ECHINODERMATA	12.7	3.1	10.7	8.9	3.7	0.3	0.1	—	4.4
Crinoidea	—	<0.1	<0.1	—	—	—	—	—	<0.1
Holothuroidea	8.2	0.2	0.8	0.8	0.2	0.1	0.1	—	0.3
Echinoidea	1.2	1.3	0.1	0.1	0.1	—	—	—	1.0
Ophiuroidea	3.3	1.5	9.7	7.9	3.3	0.2	—	—	3.0
Asteroidea	—	0.1	0.1	0.2	0.1	—	—	—	0.1
HEMICHORDATA	—	<0.1	<0.1	<0.1	—	—	—	—	<0.1
CHORDATA	—	1.1	0.5	0.6	—	0.2	—	—	1.0
Ascidiacea	—	1.1	0.5	0.6	—	0.2	—	—	1.0
UNIDENTIFIED	—	0.3	0.9	0.7	0.3	0.2	—	25.0	0.4
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 28

Mean wet weight of specimens of each taxon (grams per square meter) in relation to sediment organic carbon content.

Taxon	Sediment organic carbon content (percent)								
	0.00	0.01–0.49	0.50–0.99	1.00–1.49	1.50–1.99	2.00–2.99	3.00–4.99	5.00+	All ranges
PORIFERA	0.03	5.19	0.12	0.01	<0.01	—	—	—	2.98
COELENTERATA	—	6.33	18.48	14.57	1.80	0.06	—	—	9.57
Hydrozoa	—	1.06	0.16	0.01	<0.01	0.02	—	—	0.64
Anthozoa	—	5.27	18.32	14.56	1.80	0.04	—	—	8.93
Alcyonaria	—	0.26	0.32	0.13	—	—	—	—	0.24
Zoantharia	—	4.91	17.21	14.07	1.79	0.04	—	—	8.42
Unidentified	—	0.10	0.79	0.36	0.01	—	—	—	0.28
PLATYHELMINTHES	—	<0.01	<0.01	—	—	0.19	—	—	0.01
Turbellaria	—	<0.01	<0.01	—	—	0.19	—	—	0.01
NEMERTEA	0.53	0.79	0.79	0.38	0.94	0.48	—	—	0.74
ASCHELMINTHES	—	0.01	<0.01	0.02	<0.01	—	—	—	0.01
Nematoda	—	0.01	<0.01	0.02	<0.01	—	—	—	0.01
ANNELIDA	7.43	15.93	14.88	12.92	26.92	22.60	11.31	0.11	16.01
POGONOPHORA	—	<0.01	0.01	0.01	<0.01	—	—	—	<0.01
SIPUNCULIDA	0.02	0.93	1.13	0.07	<0.01	—	—	—	0.79
ECHIURA	—	0.01	1.25	1.35	—	—	—	—	0.44
PRIAPULIDA	—	<0.01	0.02	0.01	—	—	—	—	0.01
MOLLUSCA	0.80	132.21	25.23	19.95	13.38	811.54	226.87	—	99.58
Polyplacophora	—	0.25	0.03	0.02	<0.01	—	—	—	0.15
Gastropoda	0.02	3.83	0.56	0.28	1.09	10.42	—	—	2.59
Bivalvia	0.67	127.81	24.42	19.17	12.05	801.02	226.87	—	96.54
Scaphopoda	0.11	0.31	0.19	0.48	0.24	0.10	—	—	0.29
Cephalopoda	—	0.01	0.03	—	—	—	—	—	0.01
Unidentified	—	—	<0.01	—	—	—	—	—	<0.01
ARTHROPODA	0.31	13.28	6.46	1.22	1.02	18.99	9.44	0.11	9.62
Pycnogonida	—	0.01	0.01	<0.01	—	—	—	—	<0.01
Arachnida	—	<0.01	—	—	—	—	—	—	<0.01
Crustacea	0.31	13.27	6.45	1.22	1.02	18.99	9.44	0.11	9.61
Ostracoda	—	<0.01	<0.01	—	—	—	—	—	<0.01
Cirripedia	—	6.45	4.11	—	—	14.32	1.10	—	4.86
Copepoda	—	<0.01	<0.01	<0.01	—	—	—	—	<0.01
Cumacea	0.03	0.09	0.03	0.02	0.01	0.24	—	—	0.07
Tanaidacea	—	<0.01	<0.01	—	—	—	—	—	<0.01
Isopoda	0.19	0.27	0.24	0.03	0.14	0.06	0.05	—	0.23
Amphipoda	0.09	5.29	1.76	0.59	0.17	0.21	8.29	0.11	3.54
Mysidacea	—	0.01	0.01	—	0.01	0.01	—	—	0.01
Decapoda	—	1.16	0.30	0.58	0.69	4.15	—	—	0.91
Unidentified	—	<0.01	<0.01	—	—	—	—	—	<0.01
BRYOZOA	0.23	1.95	0.02	0.06	1.21	—	0.18	—	1.19
BRACHIOPODA	1.31	0.96	1.74	0.03	—	—	—	—	0.95
ECHINODERMATA	6.16	35.22	23.25	44.01	43.35	104.47	561.51	—	38.82
Crinoidea	—	<0.01	<0.01	—	—	—	—	—	<0.01
Holothuroidea	5.80	3.97	11.16	30.95	40.90	104.31	561.51	—	15.66
Echinoidea	0.29	27.90	5.44	1.33	0.60	—	—	—	17.29
Ophiuroidea	0.07	2.32	5.23	6.28	0.56	0.16	—	—	3.26
Asteroidea	—	1.03	1.42	5.45	1.29	—	—	—	1.61
HEMICHORDATA	—	0.03	0.03	<0.01	—	—	—	—	0.03
CHORDATA	—	4.38	1.88	2.03	—	0.33	—	—	3.15
Ascidiacea	—	4.38	1.88	2.03	—	0.33	—	—	3.15
UNIDENTIFIED	—	0.33	0.27	0.29	0.10	0.07	—	0.11	0.29
Total	16.82	217.56	95.95	96.93	88.72	958.73	809.31	0.33	183.18

Table 29

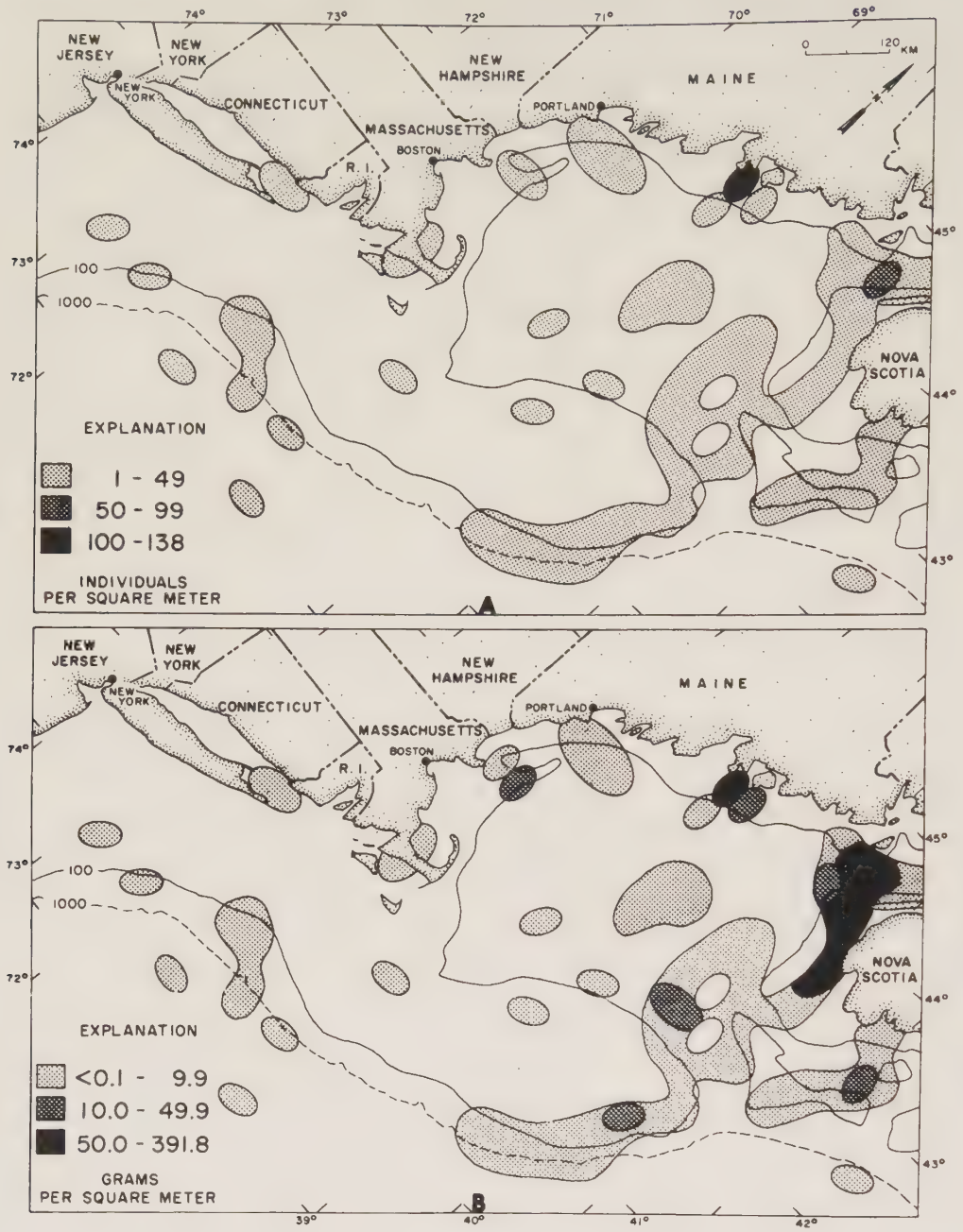
The wet weight of specimens of each taxon, expressed as a percentage of the total benthic invertebrate fauna, in relation to sediment organic carbon content.

Taxon	Sediment organic carbon content (percent)								
	0.00	0.01–0.49	0.50–0.99	1.00–1.49	1.50–1.99	2.00–2.99	3.00–4.99	5.00+	All ranges
PORIFERA	0.2	2.4	0.1	<0.1	<0.1	—	—	—	1.6
COELENTERATA	—	2.9	19.3	15.0	2.0	<0.1	—	—	5.2
Hydrozoa	—	0.5	0.2	<0.1	<0.1	<0.1	—	—	0.3
Anthozoa	—	2.4	19.1	15.0	2.0	<0.1	—	—	4.9
Alcyonaria	—	0.1	0.3	0.1	—	—	—	—	0.1
Zoantharia	—	2.3	18.0	14.5	2.0	<0.1	—	—	4.6
Unidentified	—	<0.1	0.8	0.4	<0.1	—	—	—	0.2
PLATYHELMINTHES	—	<0.1	<0.1	—	—	<0.1	—	—	<0.1
Turbellaria	—	<0.1	<0.1	—	—	<0.1	—	—	<0.1
NEMERTEA	3.2	0.4	0.8	0.4	1.1	<0.1	—	—	0.4
ASCHELMINTHES	—	<0.1	<0.1	<0.1	<0.1	—	—	—	<0.1
Nematoda	—	<0.1	<0.1	<0.1	<0.1	—	—	—	<0.1
ANNELIDA	44.2	7.3	15.6	13.3	30.3	2.4	1.4	33.3	8.7
POGONOPHORA	—	<0.1	<0.1	<0.1	<0.1	—	—	—	<0.1
SIPUNCULIDA	0.1	0.4	1.2	0.1	<0.1	—	—	—	0.4
ECHIURA	—	<0.1	1.3	1.4	—	—	—	—	0.2
PRIAPULIDA	—	<0.1	<0.1	<0.1	—	—	—	—	<0.1
MOLLUSCA	4.7	60.8	26.4	20.6	15.1	84.7	28.0	—	54.4
Polyplacophora	—	0.1	<0.1	<0.1	<0.1	—	—	—	0.1
Gastropoda	0.1	1.8	0.6	0.3	1.2	1.1	—	—	1.4
Bivalvia	4.0	58.7	25.6	19.8	13.6	83.6	28.0	—	52.7
Scaphopoda	0.6	0.1	0.2	0.5	0.3	<0.1	—	—	0.2
Cephalopoda	—	<0.1	<0.1	—	—	—	—	—	<0.1
Unidentified	—	—	<0.1	—	—	—	—	—	<0.1
ARTHROPODA	1.8	6.1	6.8	1.3	1.2	1.9	1.2	—	5.2
Pycnogonida	—	<0.1	<0.1	<0.1	—	—	—	—	<0.1
Arachnida	—	<0.1	—	—	—	—	—	—	<0.1
Crustacea	1.8	6.1	6.8	1.3	1.2	1.9	1.2	33.3	5.2
Ostracoda	—	<0.1	<0.1	—	—	—	—	—	<0.1
Cirripedia	—	3.0	4.3	—	—	1.5	0.1	—	2.7
Copepoda	—	<0.1	<0.1	<0.1	—	—	—	—	<0.1
Cumacea	0.2	<0.1	<0.1	<0.1	<0.1	<0.1	—	—	<0.1
Tanaidacea	—	<0.1	<0.1	—	—	—	—	—	<0.1
Isopoda	1.0	0.1	0.3	<0.1	0.2	<0.1	<0.1	—	<0.1
Amphipoda	0.5	2.4	1.8	0.6	0.2	<0.1	1.0	33.3	1.9
Mysidacea	—	<0.1	<0.1	—	<0.1	<0.1	—	—	<0.1
Decapoda	—	0.5	0.3	0.6	0.8	0.4	—	—	0.5
Unidentified	—	<0.1	<0.1	—	—	—	—	—	<0.1
BRYOZOA	1.4	0.9	<0.1	0.1	1.4	—	<0.1	—	0.7
BRACHIOPODA	7.8	0.4	1.8	<0.1	—	—	—	—	0.5
ECHINODERMATA	36.6	16.2	24.4	45.4	48.8	10.9	69.4	—	20.7
Crinoidea	—	<0.1	<0.1	—	—	—	—	—	<0.1
Holothuroidea	34.5	1.8	11.7	31.9	46.0	10.9	69.4	—	8.6
Echinoidea	1.7	12.8	5.7	1.4	0.7	—	—	—	9.4
Ophiuroidea	0.4	1.1	5.5	6.5	0.6	<0.1	—	—	1.8
Asteroidea	—	0.5	1.5	5.6	1.5	—	—	—	0.9
HEMICHORDATA	—	<0.1	<0.1	<0.1	—	—	—	—	<0.1
CHORDATA	—	2.0	2.0	2.1	—	<0.1	—	—	1.7
Ascidiacea	—	2.0	2.0	2.1	—	<0.1	—	—	1.7
UNIDENTIFIED	—	0.2	0.3	0.3	0.1	<0.1	—	33.3	0.2
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 30

Frequency of occurrence (%) of each taxonomic group in the samples in each sediment organic carbon content class.

Taxon	Sediment organic carbon content (percent)							
	0.00	0.01–0.49	0.50–0.99	1.00–1.49	1.50–1.99	2.00–2.99	3.00–4.99	5.00+
PORIFERA	20	11	6	2	2	—	—	—
COELENTERATA	—	53	57	37	26	30	—	—
Hydrozoa	—	19	5	4	5	15	—	—
Anthozoa	—	35	52	33	21	15	—	—
Alcyonaria	—	5	14	8	—	15	—	—
Zoantharia	—	26	29	23	21	15	—	—
PLATYHELMINTHES	—	2	1	—	—	8	—	—
Turbellaria	—	2	1	—	—	8	—	—
NEMERTEA	40	46	45	39	23	15	—	—
ASCHELMINTHES	—	10	8	17	7	—	—	—
Nematoda	—	10	8	17	7	—	—	—
ANNELIDA	80	98	99	100	98	100	50	100
POGONOPHORA	—	2	21	10	2	—	—	—
SIPUNCULIDA	20	31	28	8	2	—	—	—
ECHIURA	—	<1	7	4	—	—	—	—
PRIAPULIDA	—	<1	1	1	—	—	—	—
MOLLUSCA	100	90	96	98	91	100	75	—
Polyplacophora	—	10	12	8	2	—	—	—
Gastropoda	20	51	47	49	61	31	—	—
Bivalvia	80	85	94	99	88	100	75	—
Scaphopoda	20	17	31	32	28	15	—	—
Cephalopoda	—	1	1	—	—	—	—	—
ARTHROPODA	100	98	85	67	61	77	50	100
Pycnogonida	—	3	2	1	—	—	—	—
Arachnida	—	<1	—	—	—	—	—	—
Crustacea	100	95	83	66	61	77	50	100
Ostracoda	—	1	1	—	—	—	—	—
Cirripedia	—	6	3	—	—	15	25	—
Copepoda	—	1	1	1	—	—	—	—
Cumacea	20	44	29	23	12	31	—	—
Tanaidacea	—	1	7	—	—	—	—	—
Isopoda	20	47	27	11	5	15	25	—
Amphipoda	60	93	72	55	49	62	50	100
Mysidacea	—	5	3	—	7	8	—	—
Decapoda	—	32	9	4	5	23	—	—
BRYOZOA	20	16	7	4	5	—	25	—
BRACHIOPODA	40	6	5	2	—	—	—	—
ECHINODERMATA	100	70	83	76	63	31	25	—
Crinoidea	—	<1	1	—	—	—	—	—
Holothuroidea	40	17	37	27	16	15	25	—
Echinoidea	20	34	14	6	12	—	—	—
Ophiuroidea	60	39	70	66	47	23	—	—
Asteroidea	—	14	17	14	7	—	—	—
HEMICHORDATA	—	1	1	1	—	—	—	—
CHORDATA	—	23	19	13	—	8	—	—
Ascidiacea	—	23	19	13	—	8	—	—



PORIFERA

Figure 27

Geographic distribution of Porifera: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

fauna was moderately high (3–5%) along the outer continental shelf and upper continental slope (Table 14). On the inner shelf and in very deep water, sponges made up a small portion of the total biomass.

Sponges were present in 3 to 12% of the collections within each depth class (Table 15). The highest frequency of occurrence was on the continental slope (200 to 2,000 m). These sponges were small, and were frequently attached to polychaete tubes, shell fragments, corals, and other biogenic substrates.

Relation to Sediments

Porifera were generally more numerous and constituted a substantially larger biomass in coarse substrates

(gravel, till, and shell) than in those composed of fine particles (Tables 16–20; Fig. 30). Also, the proportion of samples containing Porifera was higher for the coarse than the fine substrates. Till contained the highest density of specimens, the greatest weight, and highest frequency of occurrence. Gravel ranked second in number and shell ranked second in weight. Sand contained intermediate quantities, and sand-silt and silt-clay contained the smallest quantities.

Relation to Water Temperature

Porifera were generally most numerous in areas where the annual range in bottom water temperature was moderate—4° to 12°C (Tables 21–25; Fig. 31). Where the annual temperature excursions were less than 4° or greater than 12°C the average biomass was markedly lower than at midrange. The frequency of occurrence was highest (15%) in those samples from localities in which the seasonal changes in temperature were between 4° and 8°C.

Two other aspects of the relative density of Porifera and bottom water temperature that were examined, but not tabulated or illustrated here, concern annual maximum and annual minimum temperature. Sponges were more plentiful (2 to 7 g/m^2) in areas where the maximum temperature was moderate, between 6° and 12°C; they were scarce (<1 g/m^2) where the maximum temperature remained below 6° or rose above 12°C. Porifera were abundant (>4 g/m^2) where the minimum temperature was low (0° to 3.9°C) and scarce (<1 g/m^2) where the minimum temperature was high.

Relation to Sediment Organic Carbon

Porifera were found only where sediments contained low to moderate (0.01 to 1.99%) amounts of organic carbon (Tables 26–30; Fig. 32). Both mean density and biomass diminished with increasing organic carbon content. Density ranged from 3 to 0.2/m^2, and biomass from 5 to <0.01 g/m^2.

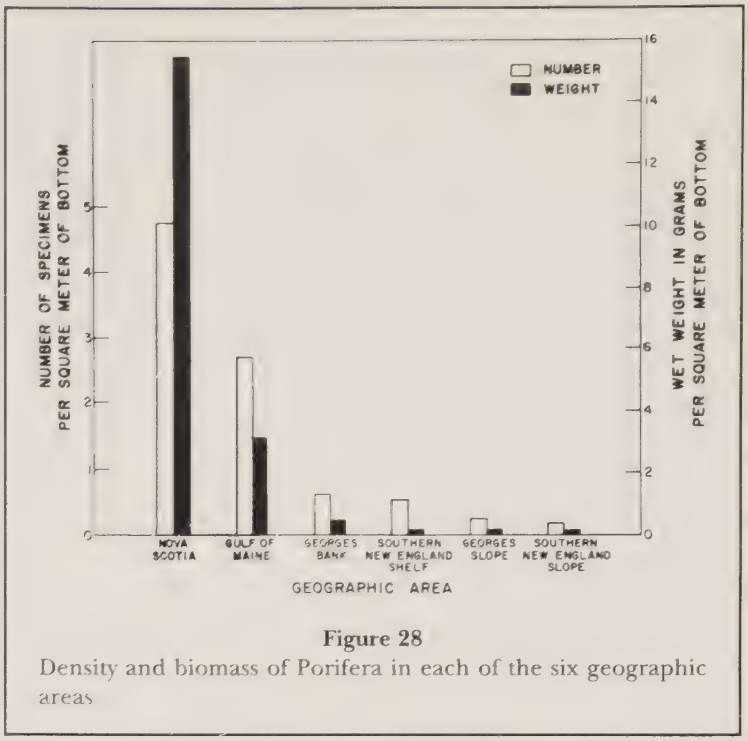


Figure 28
Density and biomass of Porifera in each of the six geographic areas

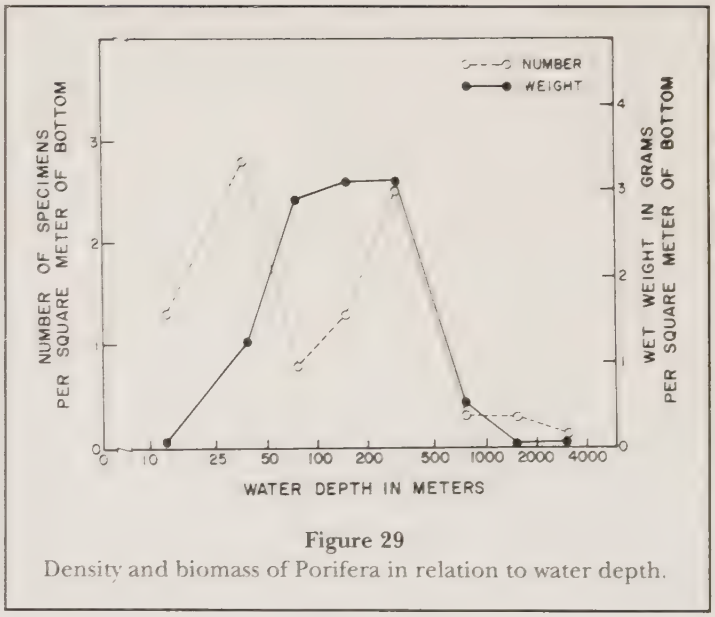

NUMBER
WEIGHT
NUMBER OF SPECIMENS PER SQUARE METER OF BOTTOM
WET WEIGHT IN GRAMS PER SQUARE METER OF BOTTOM
0 10 25 50 100 200 500 1000 2000 4000
WATER DEPTH IN METERS

Figure 29
Density and biomass of Porifera in relation to water depth.

Coelenterata

The macrobenthic coelenterate fauna of the New England region is composed of members of two classes: Hydrozoa and Anthozoa. Hydrozoa are treated at the class level, whereas Anthozoa, composed of members from seven orders contained in two subclasses, are discussed at the subclass levels: Alcyonaria and Zoantharia.

No discussions are included at the taxonomic levels Coelenterata or Anthozoa; however, the interested reader will find summary data, for all treated parameters, for those taxonomic levels in Tables 5–30.

Hydrozoa—Hydrozoans were common in parts of the New England region, but their limited occurrence and moderately small size severely restricted their contribution to the total biomass. They made up less than 1% of

the benthic biomass (Table 3). Members of this group were most abundant in shallow waters and were attached to firm substrates, frequently where water currents were moderate to strong.

Hydrozoans in our samples were small in size and delicately tinted in white, pink, violet, tan, and brown. They were exclusively carnivores preying on planktonic crustaceans and other small animals carried to them by water currents. In turn, hydrozoans are preyed upon by nudibranchs and, probably, other omnivores and carnivores.

The most common forms encountered were Leptomedusae, represented by the genera *Campanularia*, *Sertularia*, *Obelia*, and others. Less common were representatives of Anthomedusae, of which *Hydractinia* is a member. This hydrozoan occurred on live mollusks and on dead shell. Some encrusted gastropod shells were inhabited by hermit crabs.

Hydrozoans occurred in 126 samples (12% of total); their average density was 6.4/m^2 and biomass averaged 0.5 g/m^2 (Table 5).

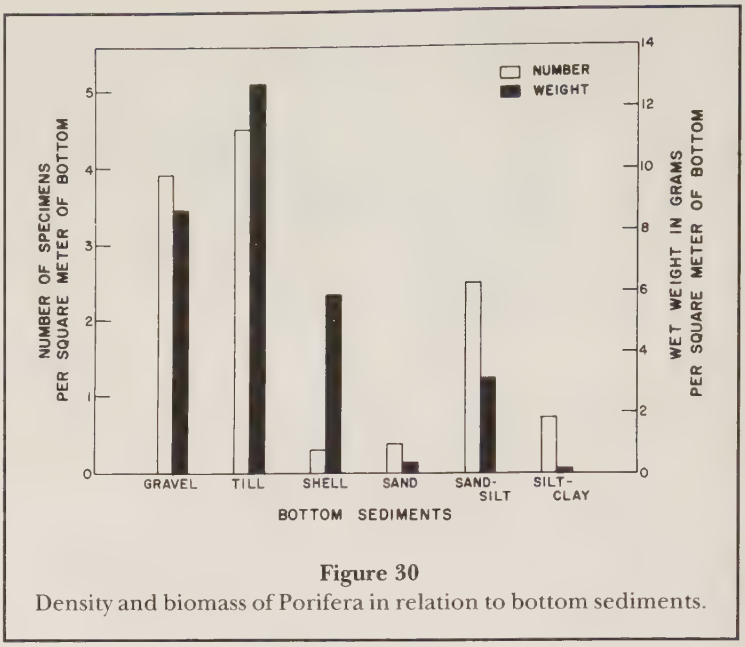


Figure 30
Density and biomass of Porifera in relation to bottom sediments.

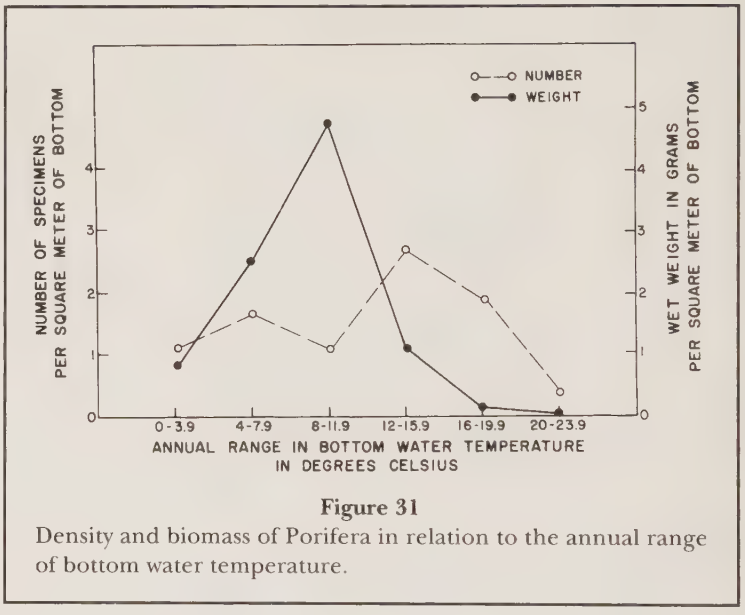


Figure 31
Density and biomass of Porifera in relation to the annual range of bottom water temperature.

Geographic Distribution

Hydrozoans were common in coastal areas and on offshore banks (Fig. 33). They were absent, or present in only small quantities, in much of the central sections of the Gulf of Maine, in large areas of the continental shelf south of Rhode Island, and on the continental slope and rise. High densities, 100 to 500 colonies/m^2, and high biomass, 10 to 45 g/m^2, occurred in only a few scattered localities. Low densities, to 49 colonies/m^2, and average weights less than 1 g/m^2 were much more common and widely distributed.

Three geographic areas contained moderate to large quantities of hydrozoans: Nova Scotia, Georges Bank, and the Southern New England Shelf (Tables 6, 8; Fig. 34). Average densities in these areas ranged from 7 to 12 colonies/m^2; biomass averaged from 0.4 to 1.6 g/m^2. Georges Bank ranked first in terms of weight, and Nova Scotia ranked first in number of specimens. Small quantities of hydrozoans were found in the Gulf of Maine, Georges Slope, and Southern New England Slope. Quantities in these three areas averaged between 3.3 and 0.1 colonies/m^2, and 0.12 and <0.1 g/m^2.

The frequency of occurrence of hydrozoans in the samples (Table 10) indicates the same general trend of abundance as the average number and weight of specimens. Percentages of samples containing hydrozoans ranged from a high of 29% in the Nova Scotia area (8 to 15% in the other shelf areas) to a low frequency (1 to 4%) in the Georges Slope and Southern New England Slope area.

Bathymetric Distribution

Hydrozoans were most abundant in shallow water (0–24 m) where their density averaged 37 colonies/m^2 and they diminished in quantity more or less directly with increased depth (Tables 11, 12; Fig. 35). In deeper waters (25–200 m) that cover the offshore continental shelf, their average density was between 2 and 6 colonies/m^2. They were uncommon to rare on the continental slope and rise.

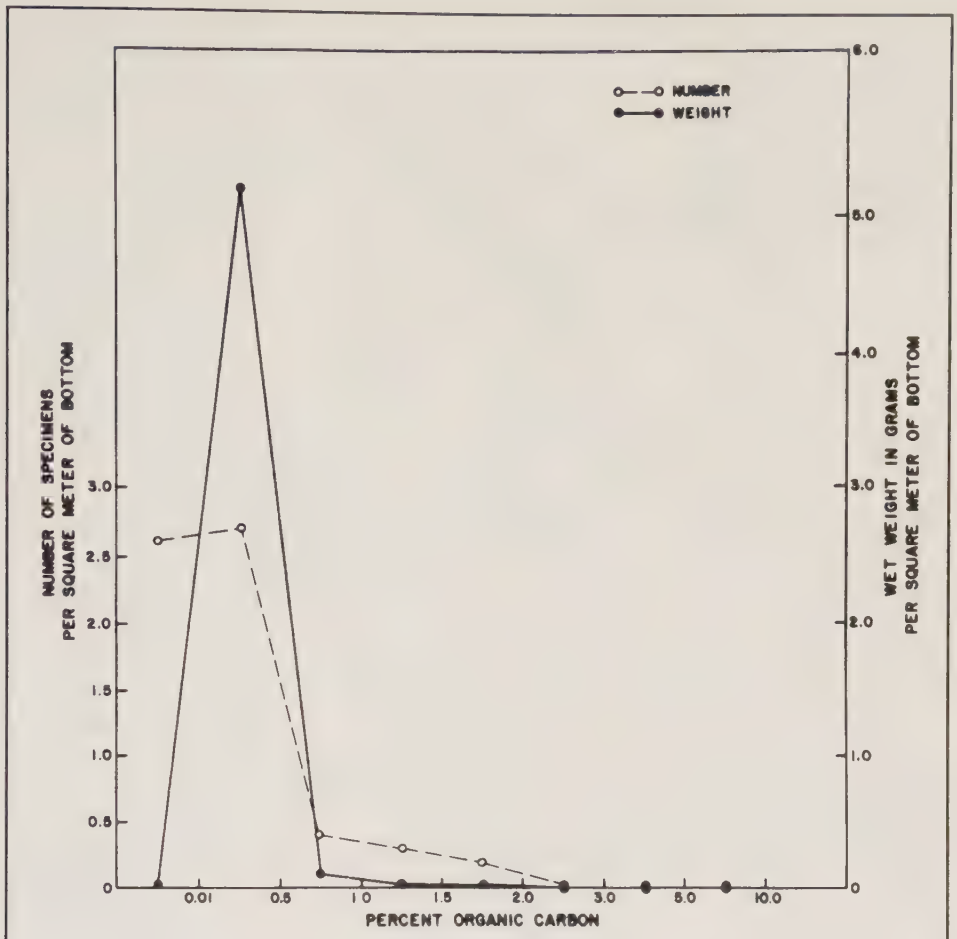


Figure 32
Density and biomass of Porifera in relation to sediment organic carbon.

Biomass trends were the same as those described above for numerical density, with the exception of unusually large quantities between 50 and 100 meters (Tables 13, 14; Fig. 35). In the shallow zone (0–24 m) the average weight was 1.2 g/m^2. In deeper water, at a depth of 1,000 m and greater, the average quantity decreased to <0.01 g/m^2. The extraordinarily large quantity between 50 and 100 m resulted from relatively few very large colonies.

The frequency of occurrence of hydroids in samples was highest (21%) in the shallow water zone (0–24 m), dropping to 3% at depths below 1,000 m (Table 15).

Relation to Bottom Sediments

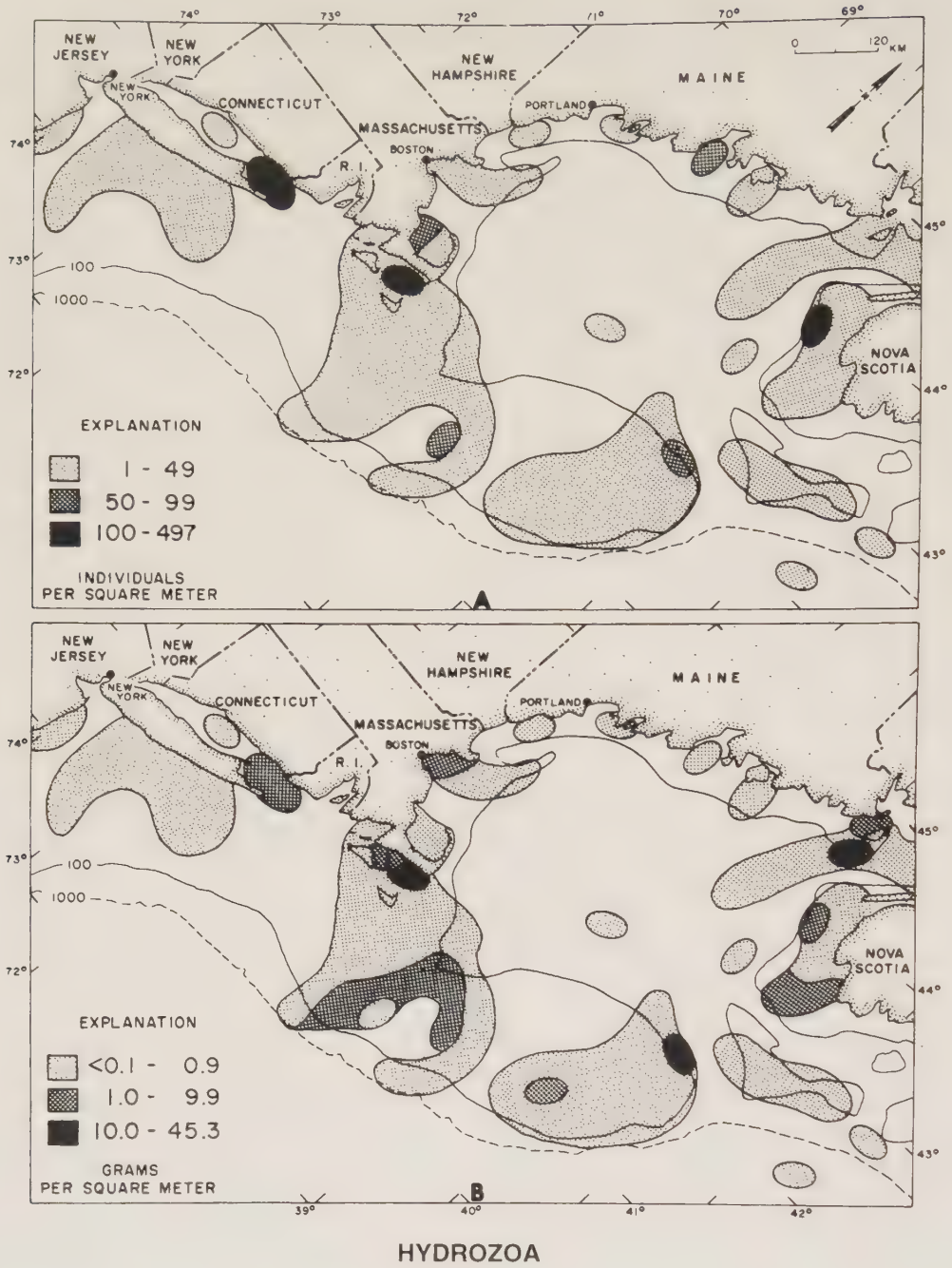
Hydrozoans occurred on all sediment types found in the region; however, they were much more prevalent on gravels than on other types of substrates (Tables 16, 18; Fig. 36). Both numerical density and weight diminished with decreased sediment particle size. Average density dropped from 20 colonies/m^2 in gravel to 2 colonies/m^2 in silt-clay. Wet weight declined from an average of 2.6 g/m^2 in gravel to 0.01 g/m^2 in silt-clay. Intermediate quantities were present on substrates composed of medium-sized particles.

Frequency of occurrence also reflected the general trend of higher densities on coarse substrates and low densities in fine-grained substrates (Table 20). In coarse sediments the percentage of samples containing hydroids ranged from 23 to 33%. The percentage occurrence in sand, an intermediate grade, was 14%. In the fine-grained sediments the frequency of occurrence was only 4 to 6%.

Hydrozoans constituted only a small part (1.4%) of the total benthic fauna, even in the sediment type (gravel) in which they were most abundant (Table 19).

Relation to Water Temperature

The density of hydroids increased as the annual range in bottom water temperature broadened. Average density



HYDROZOA

Figure 33

Geographic distribution of Hydrozoa: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

was only 0.9 colonies/m^2 where the temperature range was small, reaching an average of 46 colonies/m^2 where the temperature range was broad (Table 21; Fig. 37), a marked increase in density occurred between the 12–15.9°C and 16–19.9°C classes: in the former the average density was 5 colonies/m^2; in the latter it was 37 colonies/m^2.

The contribution of hydroids to the total faunal density was <0.5% in the middle and low-range classes but was above 1% in the two high-range classes (Table 22).

Hydroid biomass was moderate or low in all temperature range classes and no consistent trend in relation to temperature range was evident (Tables 23, 24; Fig. 37).

Although hydroids did not occur in a large proportion of the samples, there was a general trend of increasing occurrence rate from 4% in the low-range temperature classes to 26 and 18% in the high-range temperature classes (Table 25).

Relation to Sediment Organic Carbon

Hydrozoan abundance was generally negatively correlated to the quantity of organic carbon in the sediments (Fig. 38). Density of hydroids was greatest (9 colonies/m^2) where sediment organic carbon content was low (<1%), declining to moderate levels where carbon content was between 1 and 3% (Tables 26, 27). They were absent in sediments containing the greatest amounts of organic carbon (>3%).

Biomass of hydrozoans paralleled density, diminishing with increasing organic carbon content (Tables 28, 29). Biomass ranged from slightly over 1 g/m^2 to <0.01 g/m^2.

Frequency of occurrence of hydroids in samples ranged from 4 to 19% (Table 30). The trend differed from density and biomass, however, in being parabolic with lowest occurrence in the middle ranges and increasing at each extreme.

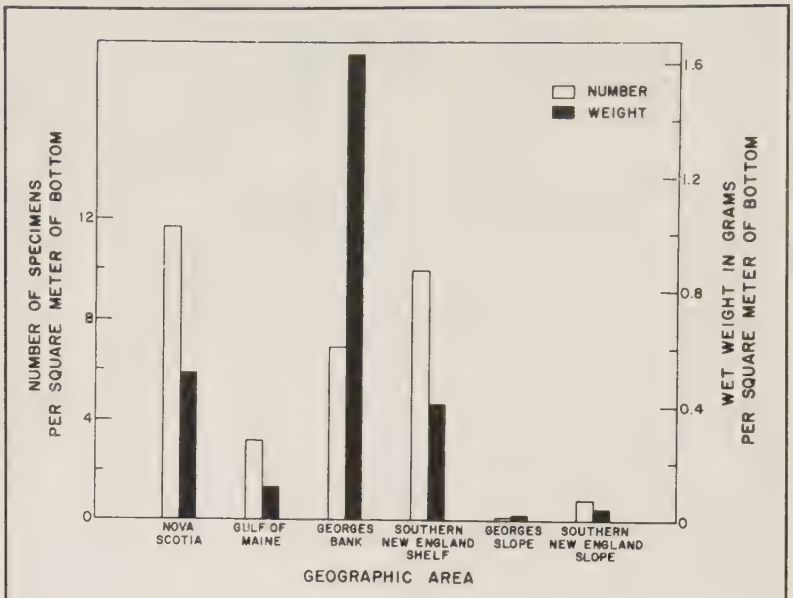


Figure 34
Density and biomass of Hydrozoa in each of the six geographic areas.

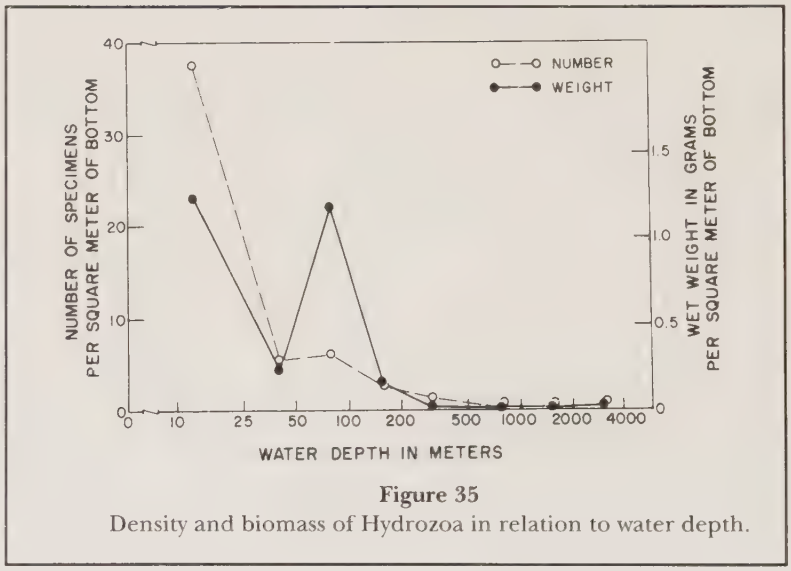


Figure 35
Density and biomass of Hydrozoa in relation to water depth.

Anthozoa—

Alcyonaria—Alcyonarian coelenterates in our samples were composed of soft corals, orders Alcyonacea and Gorgonacea, and sea pens, order Pennatulacea. Because of the limited occurrence of both groups (<0.1% of the number of all organisms), and despite their large size, they also constituted <0.1% of the total benthic biomass (Table 3). None of the alcyonarians in our samples were taken from depths less than 50 m. They were most abundant between 200 and 500 m.

Soft corals are typically bush- or treelike in shape and they attach to hard substrates, usually rock outcrops or gravel. Soft corals range in height from a few millimeters to several meters. Trunk diameters are proportional in size, and in large specimens occasionally exceed 10 cm. Thus, some species of this group may rank as the largest sessile invertebrates in this region. Colors are light tan, pink, or various dark shades of red.

Pennatulacea are feather-shaped animals commonly 10 to 25 cm in length. They characteristically dwell in soft bottom sediments anchored by a peduncle. Color of the majority of specimens in our samples was tan or a combination of light cream (rachis) and deep burgundy (pinnae).

Alcyonarians occurred in 63 samples (6% of total). Their density averaged 0.8/m^2 and biomass averaged 0.2 g/m^2 (Table 5).

Geographic Distribution

Alcyonarians were present along the outer margin of the continental shelf and on the continental slope and rise. They were sparse in all sections and their occurrence was patchy, especially in the northern section

(Fig. 39). They were absent in the samples from Georges Bank. Their average density in all localities was between 1 and 15/m^2. Their average biomass at all localities was 18.9 g/m^2 or less.

Alcyonarians were present in approximately the same quantities in all standard geographic areas, except Georges Bank where they were absent. Average densities in geographic areas where they were present ranged from 0.7 to 1.5/m^2, and average biomasses ranged from 0.03 to 0.43 g/m^2 (Tables 6–9; Fig. 40).

In addition to number and weight per unit area, another reasonably good index of abundance is the percentage of samples containing alcyonarians (Table 10). All shelf areas (Nova Scotia, Gulf of Maine, Georges Bank, and Southern New England Shelf) had a frequency of occurrence of 7% or less. The occurrence rates on Georges Slope and Southern New England Slope were 27% and 17%, respectively. Alcyonarians formed a larger share of the total benthic fauna in the latter two (slope) areas than in the shelf areas.

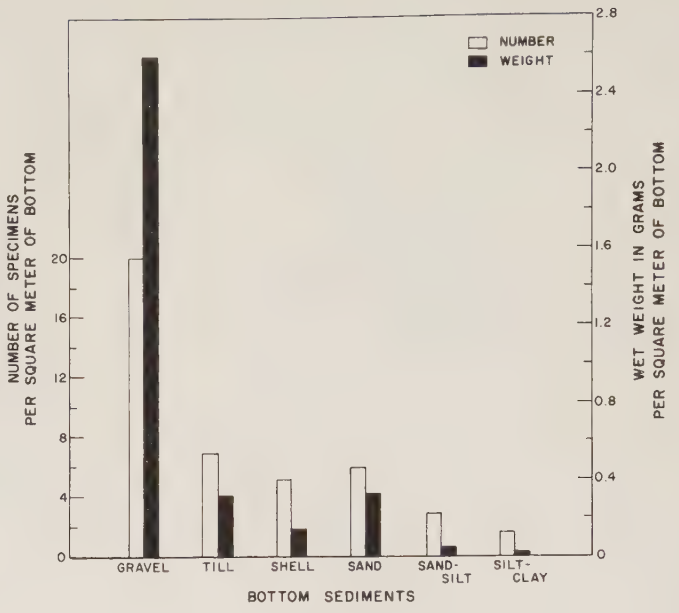


Figure 36
Density and biomass of Hydrozoa in relation to bottom sediments.

Bathymetric Distribution

Alcyonarians were most common in deep water habitats in the New England region. They were not present in any samples taken at depths less than 50 m but were represented in all depths greater than 50 m (Tables 11–14; Fig. 41). Although differences in average density and weight from one depth class to another were small, the larger quantities were most prevalent in deep water (100 to 2,000 m). Highest average density and largest average weight, 1.9/m^2 and 0.47 g/m^2, respectively, occurred at depths from 200 to 500 m.

The frequency of occurrence of alcyonarians in our shallow water (<50 m) samples was zero (Table 15). The occurrence was 5% at moderate depths (50 to 200 m) and increased to moderately high levels (22 to 29%) in deep water areas.

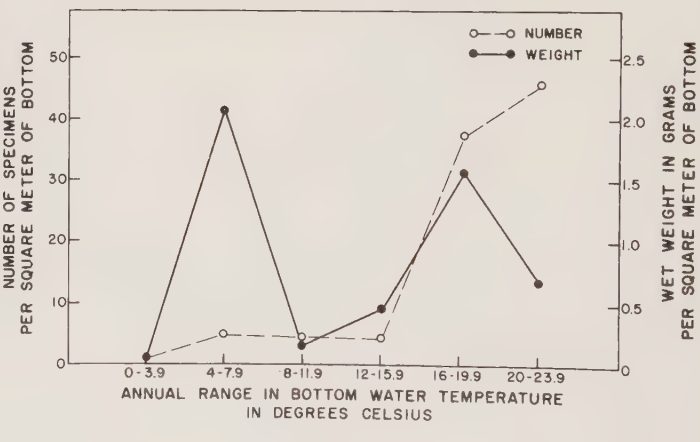


Figure 37
Density and biomass of Hydrozoa in relation to the annual range of bottom water temperature.

Relation to Bottom Sediments

Alcyonarians occurred only in selected types of substrate (Tables 16–19; Fig. 42). The Alcyonacea and Gorgonacea were collected from gravel and rocky outcrops, in contrast to the Pennatulacea, which inhabited sand-silt and silt-clay sediments. No alcyonarians were taken on substrates of till or shell, and they were present in only 5 samples out of a total of 455 from sand bottoms. Frequency of occurrence of this faunal group was highest (10 to 12%) in the silt-clay and sand-silt sediments and substantially lower (4%) in gravel (Table 20).

Relation to Water Temperature

Alcyonarians occurred only in areas where the annual temperature range was moderate or small, and less than 16°C (Tables 21–24; Fig. 43). The trends in both quantitative measures and also in frequency of occurrence exhibited a bimodal relationship.

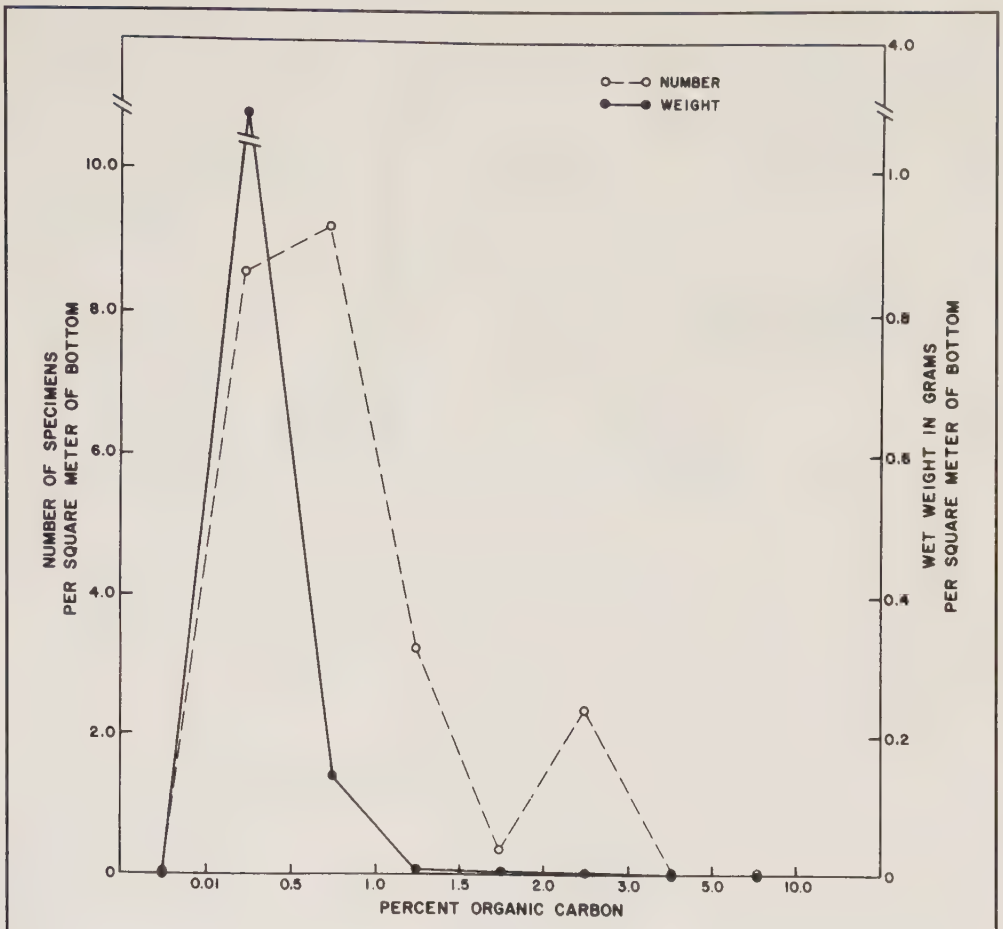


Figure 38
Density and biomass of Hydrozoa in relation to sediment organic carbon.

Alcyonarians were relatively more abundant in both the narrow (less than 4°C) temperature range class and where temperatures were moderately broad (12° to 15.9°C) than in areas of intermediate range. The densities averaged between 1.1 and 1.7/m^2 in the narrow and relatively broad range classes and between 0.2 and 1.2/m^2 in the intermediate range classes. Biomass averaged 0.31 to 0.42 g/m^2 in the narrow and relatively broad range classes and only 0.11 g/m^2 or less in the intermediate classes.

Frequency of occurrence of alcyonarians in samples ranged from 11 to 8% where the temperature was narrow and relatively broad, and only 2 to 5% in areas where the temperature range was intermediate (Table 25).

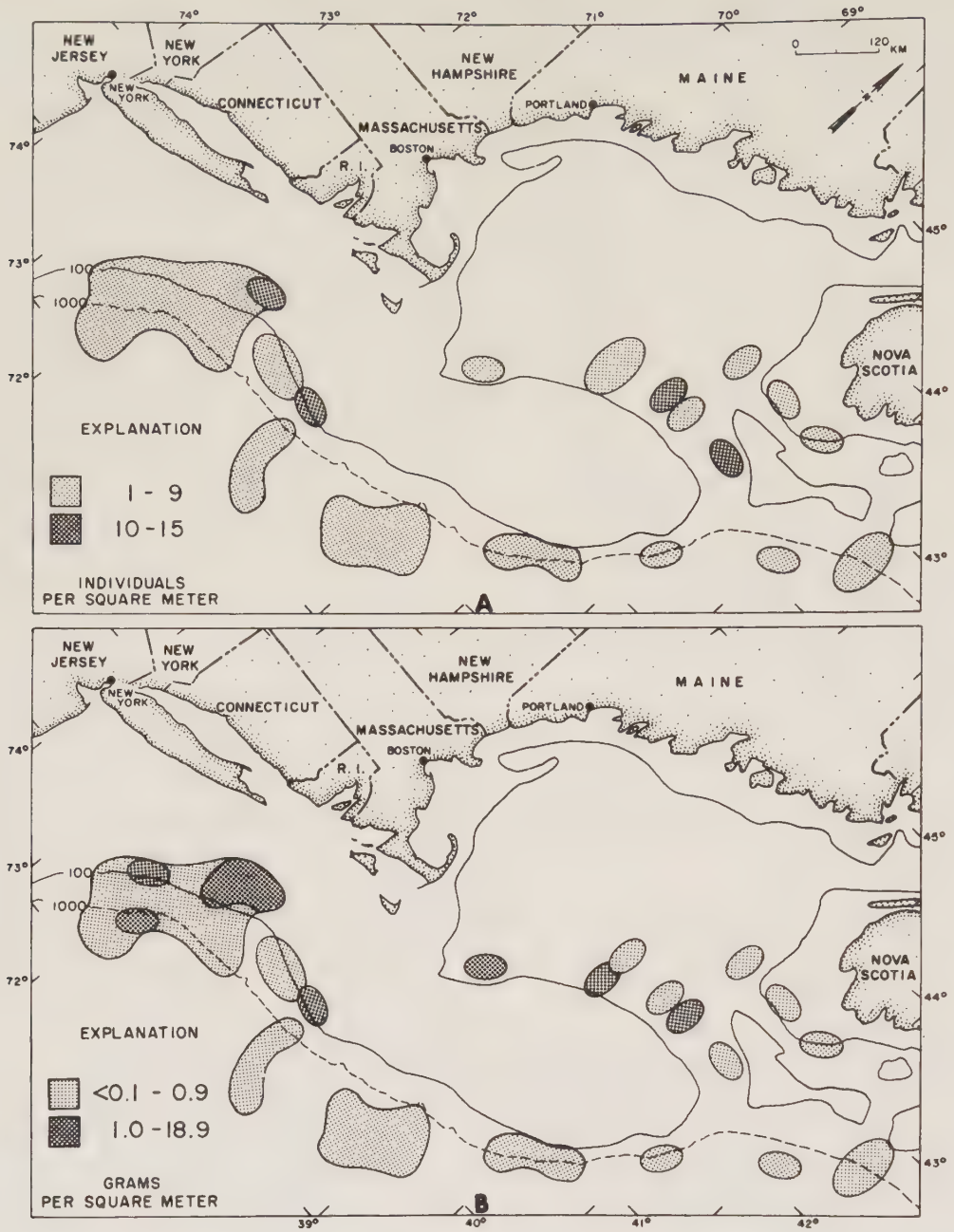
Relation to Sediment Organic Carbon

Alcyonarians occurred only in sediments with low (from 0.01 to 1.5%) organic carbon content; they were absent in areas with no measurable organic carbon, as well as in areas with carbon contents exceeding 1.5% (Fig. 44). The 0.50–0.99% carbon content class contained the highest average density (Tables 26, 27) as well as highest average biomass (Tables 28, 29). The only other carbon content classes in which alcyonarians occurred, 0.01–0.49% and 1.00–1.49%, had reduced measures of abundance.

Frequency of occurrence in samples showed a trend similar to density and biomass (Table 30), highest in the 0.50–0.99% carbon content class and significantly lower in the two adjacent classes.

Zoantharia—Four morphologically diverse orders of Zoantharia were represented in our samples from the New England region: 1) Actiniaria—sea anemones; 2) Ceriantharia—burrowing anemones; 3) Madreporaria—stony corals; and 4) Zoanthidea—colonial anemones. Altogether they contributed 1.5% of the number of animals and 3.5% of the biomass in the total macrofauna (Table 3).

Our samples contained specimens ranging in size from small (1 cm or slightly less) *Edwardsia* and other burrowing anemones to large *Cerianthus* over 30 cm in length.



ALCYONARIA

Figure 39

Geographic distribution of Alcyonaria: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

These organisms displayed many variations of color pattern and hue. Some small species and many larger forms had tentacles that were transparent or whitish. Body colors were mostly tan, flesh colored, or reddish-brown; a few were orange, red, or another somewhat similar bright color.

Stony corals of both solitary and colonial types occurred but neither type was common.

Commensalism was common among the Actiniaria and Zoanthidea, particularly in association with hermit crabs and decapod shrimps.

Occupancy of diverse habitats characterized the New England zoantharians. They occurred in a wide variety of substrates, and were distributed over broad ranges of water depth and temperature.

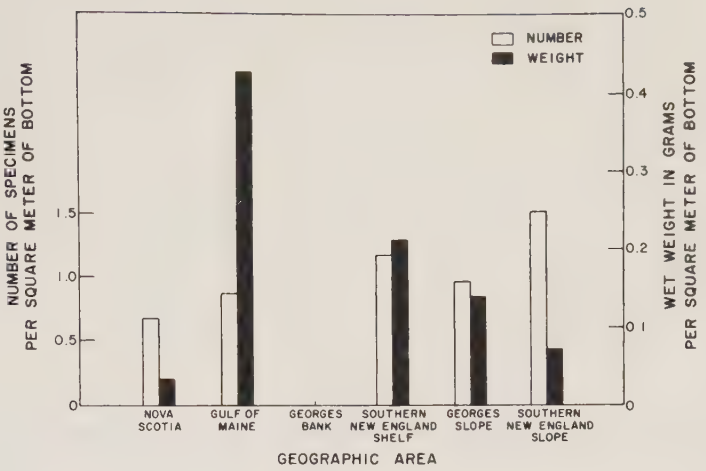


Figure 40
Density and biomass of Alcyonaria in each of the six geographic areas.

Zoantharians occurred in 265 samples (25% of the total). Their density averaged 22.6/m^2, and biomass averaged 6.4 g/m^2 (Table 5).

Geographic Distribution

Zoantharia were widely distributed over most of the marine waters off the northeastern United States (Fig. 45). They were especially common in coastal areas and on the offshore banks. Low and moderately low quantities (1 to 49 individuals, and less than 10 g/m^2 biomass) were most prevalent. Intermediate and high quantities (50 to 572 individuals, and 10 to 1,561 g/m^2 biomass) occurred in scattered patches.

Average numerical density ranged between 3 and 8.2 specimens/m^2 for all standard geographic areas except Georges Bank where the density averaged 92.5/m^2 (Tables 6, 8; Fig. 46). This unusually high abundance on the bank was due mainly to the presence of large quantities of small Ceriantharia and the moderately common Zoanthidea.

Biomass of specimens reflected entirely different patterns of abundance. Average biomass of Zoantharia within geographic areas was greatest (19.5 g/m^2) in Nova Scotia and diminished rather uniformly to the southwest (Tables 8, 9; Fig. 46), terminating with a low quantity of 0.7 g/m^2 in the southern New England Slope area.

Frequency of occurrence was moderate and fairly consistent among the various areas. The percentage of samples containing Zoantharia ranged between 17 and 31%, with the lowest incidence rates in the two slope areas (Table 10).

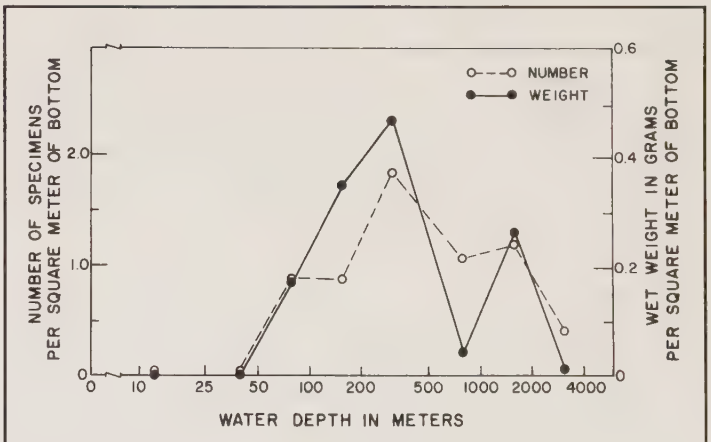


Figure 41
Density and biomass of Alcyonaria in relation to water depth.

Bathymetric Distribution

Zoantharians occurred at depths from 6 to 2,495 m but were most abundant between 25 and 100 m, where their density averaged from 21 to 91/m^2 (Tables 11, 12; Fig. 47). At other depths their density averaged 0.2 to 6.8/m^2. Only a moderate number (5.6/m^2) were present at depths from the shoreline to 24 m. Their density in deeper water progressively diminished from 6.8/m^2 in outer shelf depths to 0.2/m^2 on the continental rise.

In terms of biomass, the relationship between quantity and depth of water was considerably different from that described above for numbers of specimens. At depths of 0 to 100 m the average biomass was moderate

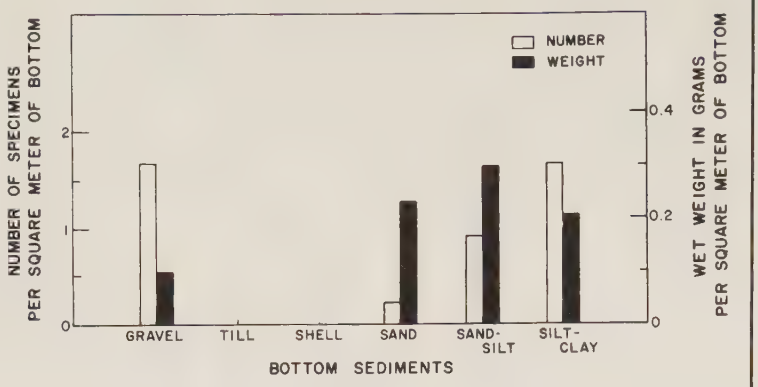


Figure 42
Density and biomass of Alcyonaria in relation to bottom sediments.

(1.2 to 2.1 g/m^2). Relatively high quantities (8 to 18 g/m^2) occurred in outer shelf and upper slope depths (Table 13; Fig. 47). The proportion of the total benthos contributed by Zoantharia was low at all depths except between 100 and 500 m where members of this group made up 13 to 19% of the total biomass (Table 14).

Frequency of occurrence of Zoantharia in samples was moderate (16 to 33%) at depths down to 500 m. At depths greater than 500 m they occurred in only 8 to 18% of the samples (Table 15).

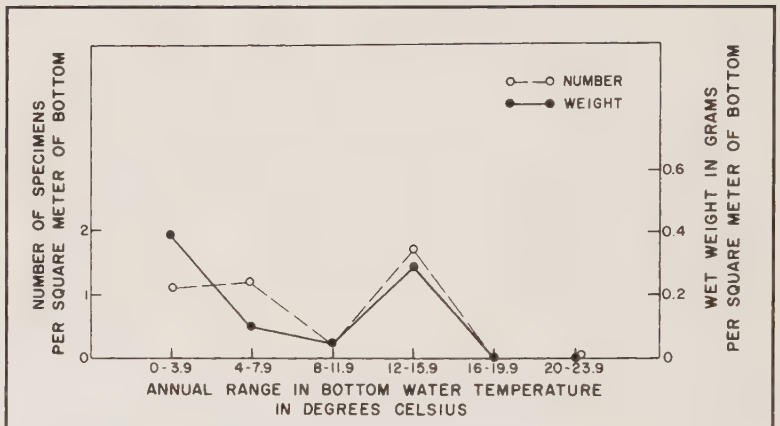


Figure 43
Density and biomass of Alcyonaria in relation to the annual range of bottom water temperature.

Relation to Sediments

Zoantharians were present in all types of bottom sediments sampled (Fig. 48). Highest density (43/m^2) occurred in sand sediments, moderate densities (9 to 14/m^2) in gravel and sand-silt, and low densities (2 to 3/m^2) in all other types (Tables 16, 17).

In terms of biomass the relationship was somewhat different. The largest quantities occurred in sand-silt, which was due mainly to the presence of large burrowing anemones. Rather large quantities, mostly actinarians, were present in gravel. Relatively small biomasses occurred in all other types of bottom sediments (Tables 18, 19).

The frequency of occurrence of this diverse group of animals was moderate and rather uniform in all types of bottom sediments. The percentage of samples containing Zoantharia in each of the different bottom types ranged from 17 to 35 (Table 20).

Relation to Water Temperature

The average density of zoantharians in relation to the annual range of bottom water temperature occurring in different regions of the study area varied from 2 to 98/m^2 (Tables 21, 22; Fig. 49). Density was highest (98/m^2) in areas with a moderate (12°–15.9°C) temperature range, and densities decreased to about 2 to 4/m^2 where the temperature range was both narrow (<4°C) and broad (>20°C).

The relation between zoantharian biomass and temperature range differed from that of density. Generally biomass was high (4 to 8 g/m^2) where the temperature range was narrow or moderately narrow (<12°C), and the general trend was a decrease in biomass associated with a broadening of the temperature range (Table 23). This correlation is revealed more clearly by the percentage of the total benthic fauna that is made up by zoantharians (Table 24). Where the temperature range was less than 4°C, zoantharians contributed 18% of the total benthos. Their contribution decreased as the temperature range broadened, forming only 0.2% of the benthos where the range was >20°C.

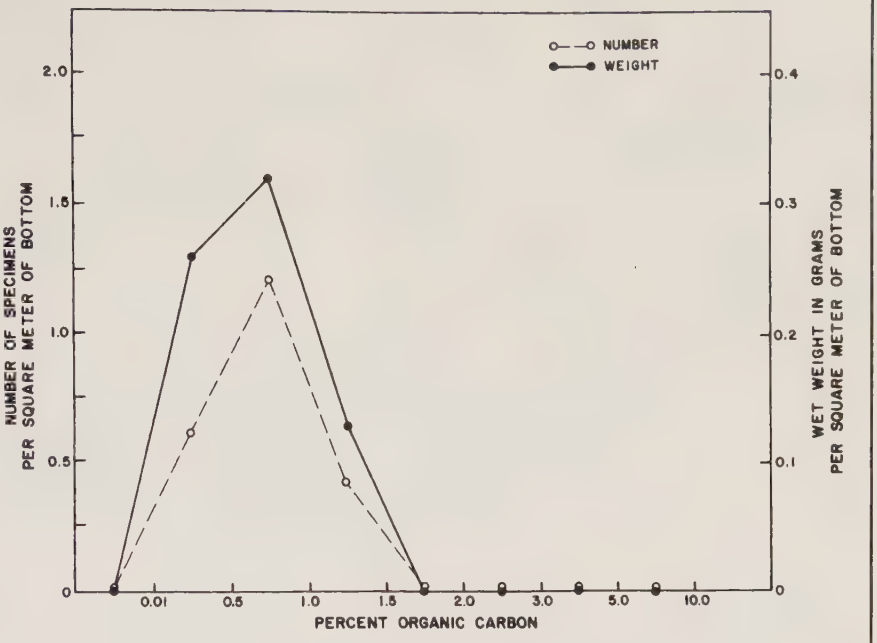


Figure 44
Density and biomass of Alcyonaria in relation to sediment organic carbon.

Frequency of occurrence was moderate under all temperature range conditions. Occurrence rates varied from 14 to 30% (Table 25). They were higher where the temperature range was moderate, and lower in the extreme (lowest and highest) range conditions.

Relation to Sediment Organic Carbon

Zoantharians occurred where sediment organic carbon content was from 0.01 to 3%; they were absent where carbon content was 0 or above 3% (Fig. 50). Density values showed a negative trend of decreasing quantity with increasing carbon content (Tables 26, 27; Fig. 50) with mean number of individuals ranging from 3 to 7/m^2.

Biomass values exhibited a somewhat similar trend with the exception that highest biomass was not in the lowest carbon content class in which they occurred (0.01–0.49%). Moderately high biomass occurred in the two classes between 0.5 and 1.5% with significantly lower levels above and below these values.

Frequency of occurrence of samples in the carbon content classes was fairly uniform, ranging from 15 to 29%, with no discernible trend as evidenced by density and biomass measures (Table 30).

Platyhelminthes

Turbellaria—Tubellarians are free-living members of the phylum Platyhelminthes. They accounted for a very small portion of the total New England benthic macrofauna. In terms of biomass and numbers of individuals they accounted for <0.1% of the total fauna (Table 3). They are small in size and those large enough to be retained on a 1-mm mesh sieving screen were present in very low density. The vast majority of marine tubellarians reported from New England marine waters are less than a few millimeters in length. Specimens in our samples ranged in size from 2 mm to nearly 2 cm in length.

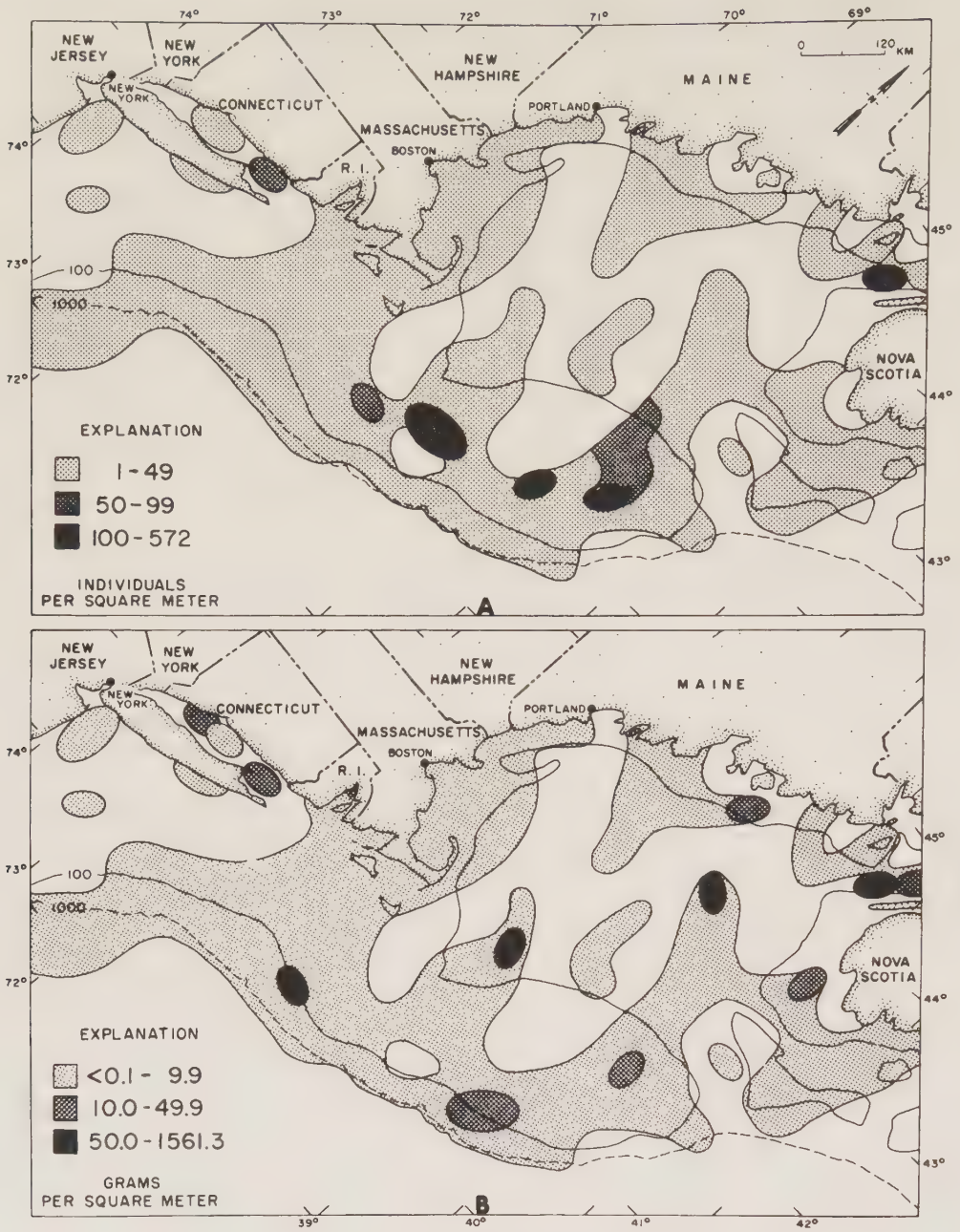
Members of this class of flatworms are free-living, soft-bodied forms and their shape varies from species to species, commonly ovoid and dorsoventrally flattened.

Turbellaria occurred in 16 samples (2% of total). Their density averaged 0.4/m^2, and their biomass averaged 0.01 g/m^2 (Table 5).

Geographic Distribution

The few Turbellaria that were present in our samples were relatively more common in the Southern New England Shelf area than in any other section (Fig. 51). Average densities as high as 59 individuals/m^2 were detected in the vicinity of Nantucket Shoals. Elsewhere densities averaged 9/m^2 or less. Members of this group were absent from large portions of the Nova Scotia Shelf, Gulf of Maine, Georges Bank, and the entire Southern New England Slope area. Average biomasses in all localities were 0.3 g/m^2 or less.

The density of turbellarians in each geographic area (Tables 6, 7; Fig. 52) averaged less than 1/m^2. The



ZOANTHARIA

Figure 45

Geographic distribution of Zoantharia: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

southern New England Shelf area contained the highest density (0.9/m^2); Georges Slope ranked second with 0.4/m^2; and all other areas had 0.2 individual or less per square meter.

The average biomass of this group of animals in each of the six geographic areas was nearly the same (Tables 8, 9; Fig. 52). The biomasses averaged 0.01 g/m^2 or less.

Frequency of occurrence also yielded a low index of abundance. Percentage of samples containing turbellarians ranged from 0 to 3% (Table 10).

Bathymetric Distribution

Turbellarians were most plentiful (2.6 specimens/m^2) in shallow water, uncommon at depths from 25 to 500

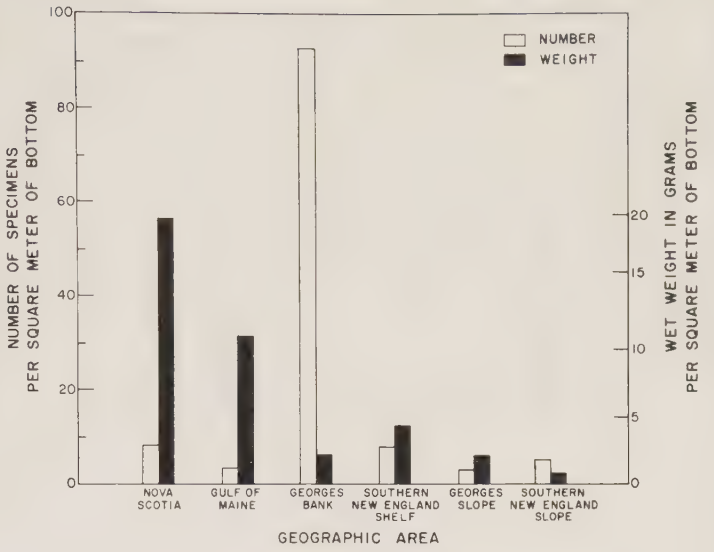


Figure 46
Density and biomass of Zoantharia in each of the six geographic areas.

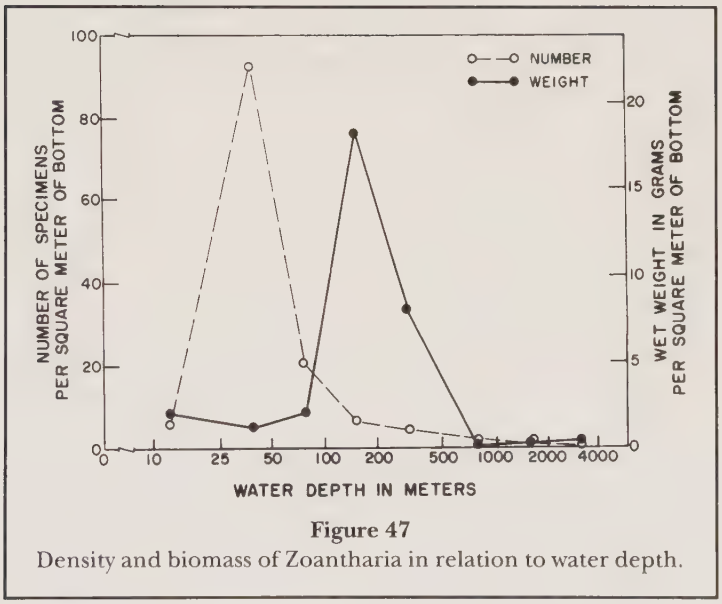


Figure 47
Density and biomass of Zoantharia in relation to water depth.

meters, and not found in depths greater than 500 meters (Tables 11, 12; Fig. 53).

Average biomass revealed a similar trend (Tables 13, 14; Fig. 53): 0.02 g/m^2 in the shallow zone and 0.01 g/m^2 or less in deeper water.

In the depth zones where they were present their incidence ranged from 1 to 4% (Table 15).

Relation to Sediments

Turbellarians were present in only three of the six major sediment types occurring in the study area. They were most common in gravel, where they averaged 1.7 individuals/m^2. In sand and silt-clay their average density was 0.2 and 0.1/m^2 (Tables 16, 17; Fig. 54).

In terms of biomass they were equally sparse (averaging 0.01 g/m^2) in all three sediment types (Tables 18, 19; Fig. 54).

Turbellarians were found in only 1 to 2% of the samples from the three sediment types in which they occurred (Table 20).

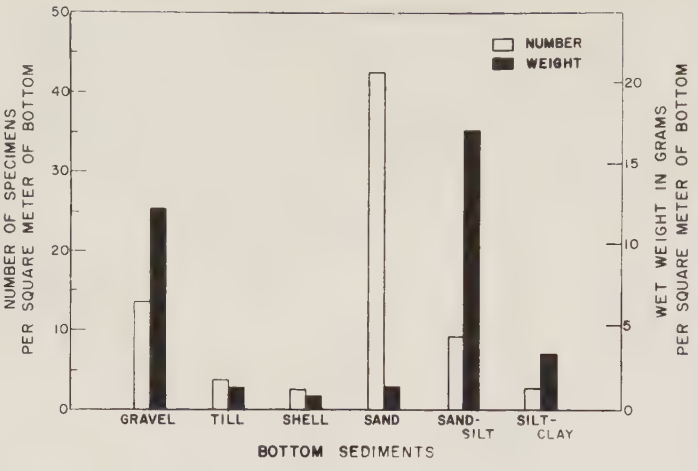


Figure 48
Density and biomass of Zoantharia in relation to bottom sediments.

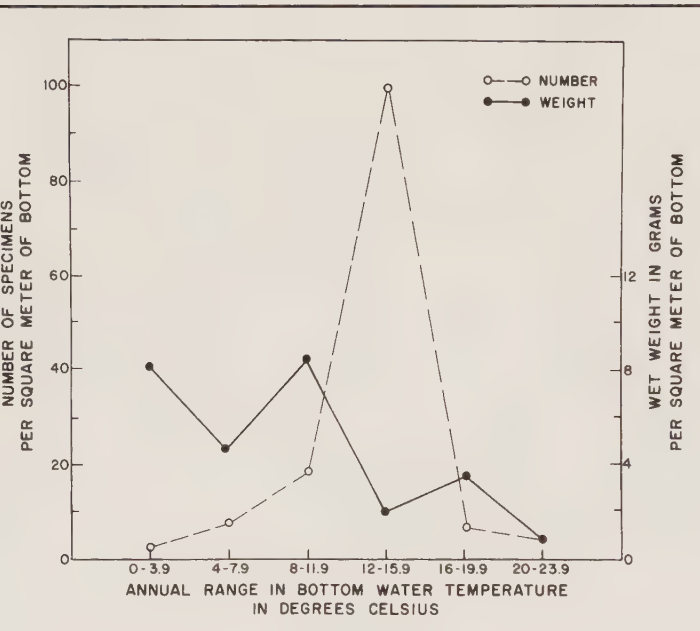


Figure 49
Density and biomass of Zoantharia in relation to the annual range of bottom water temperature.

Relation to Water Temperature

Turbellarians occurred in all temperature range classes except one (Tables 21–25; Fig. 55). They were absent from samples representing areas where the temperature change was less than 4°C. Their density, biomass, and frequency of occurrence in all temperature range classes in which they occurred were quantitatively low and roughly equal from class to class.

Relation to Ssediment Organic Carbon

Turbellarians occurred in three organic carbon content classes, two in the low range and one in the moderately high range (Fig. 56). Densities ranged from 0.1 to 0.9 individual/m^2 (Tables 26, 27), and biomasses ranged from <0.01 to 0.19 g/m^2 (Tables 28, 29). Frequency of occurrence in samples ranged from 1 to 8% (Table 30). In all measures of abundance highest values occurred

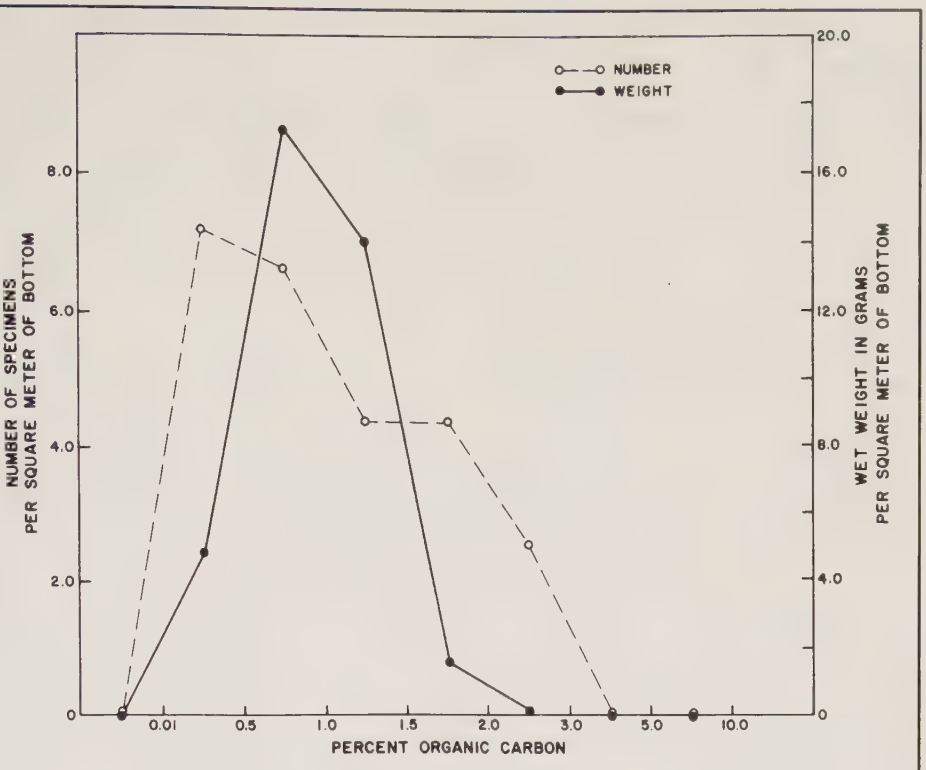


Figure 50
Density and biomass of Zoantharia in relation to sediment organic carbon.

in the moderately high (between the 2 and 3%) content class.

Nemertea

Nemertines, although widely distributed throughout the study area, made up a rather small percentage, only 0.5% of density and 0.4% of biomass, of the total benthic fauna due to their low abundance and the small size of the majority of specimens obtained (Table 3). Their greatest numerical density and biomass occurred on the continental shelf and along the upper portions of the continental slope.

Members of this group are carnivores which characteristically burrow freely in the substrate.

Specimens in our samples ranged in size from about 1 to more than 25 cm in length; however, some of the larger ones, although rare, were not whole, representing only part of an obviously larger animal. These soft-bodied, vermiform organisms easily break during the collecting process and frequently fragment when placed in formalin for preservation.

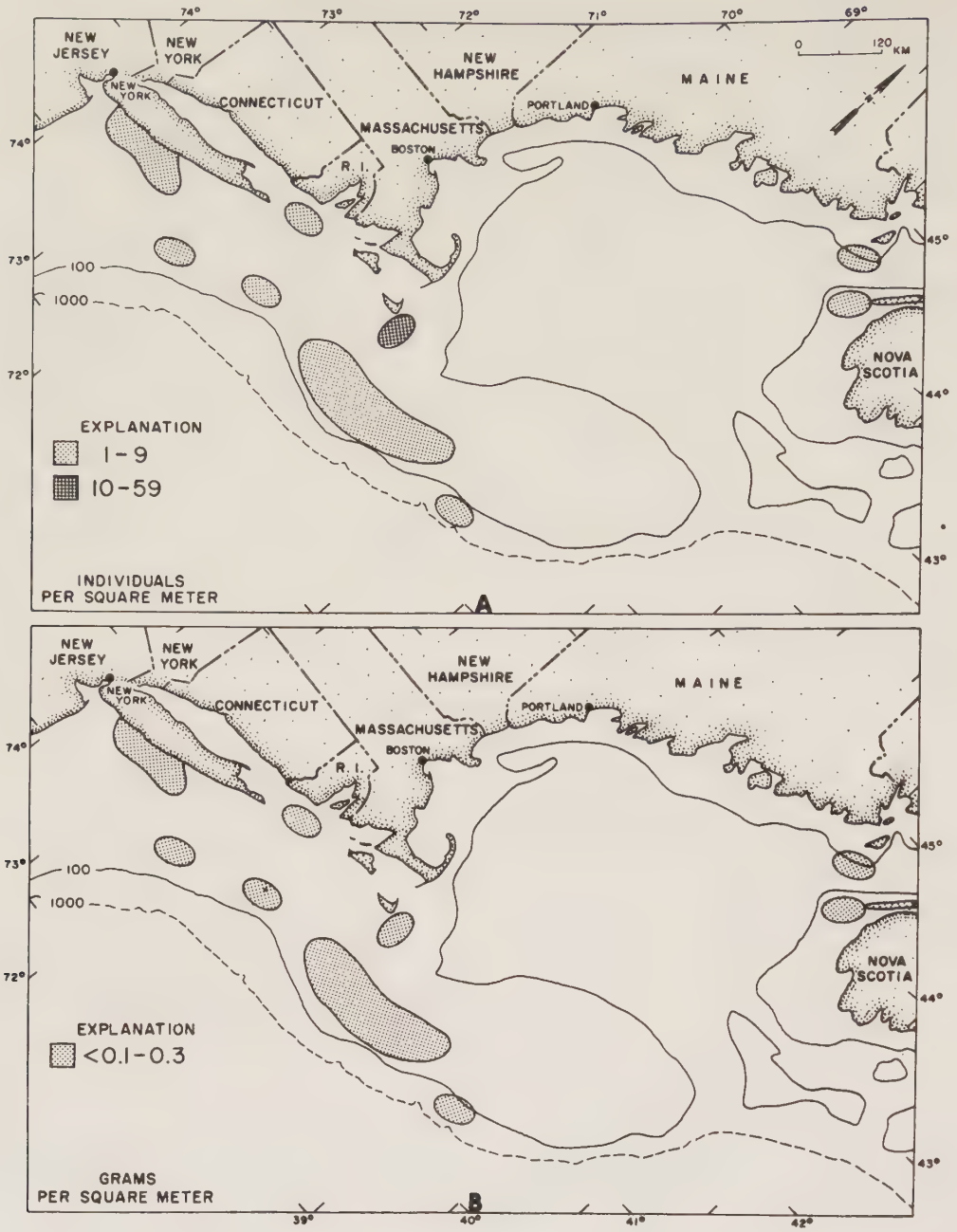
A large proportion of all specimens were uniformly tan or flesh colored. A few individuals had brownish or tan bodies with distinctive bands or stripes of white, yellow, or orange.

Although nemertines were usually represented by one or a few specimens per sample, some samples contained over 100 individuals. They occurred in 405 samples (38% of total). Their density averaged 8.2/m^2, and their biomass averaged 0.71 g/m^2 (Table 5).

Geographic Distribution

Nemertines occurred over nearly the entire study area (Fig. 57). Their numerical abundance was moderately low, averaging between 1 and 9 individuals/m^2 over most of their range. An extensive area of moderate density (10 to 49/m^2) extended along southern Georges Bank, across Great South Channel, and westward to the vicinity of Rhode Island. They were absent in a few deep water sections of the Gulf of Maine and on the continental rise southeast of Long Island, New York. Density (average number of specimens) was greatest (23 individuals/m^2) on Georges Bank (Tables 6, 7; Fig. 58). In all other areas density averaged between 1.2 and 6.8 individuals/m^2.

Over the six standard geographic areas there was a slight increase in biomass of Nemertea in the shelf areas from northeast (about 0.6 g/m^2) to southwest, with the southern New England Shelf having the largest biomass (1 g/m^2). Both slope areas had very small



TURBELLARIA

Figure 51

Geographic distribution of Turbellaria: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

quantities, averaging 0.1 and 0.2 g/m^2 (Tables 8, 9; Fig. 58).

Frequency of occurrence of nemertines was moderate in all geographic areas. They were encountered most frequently (52% of the samples) in the Southern New England Shelf. In all other areas they occurred in 25 to 35% of the samples (Table 10).

Bathymetric Distribution

Nemertea were found in water depths ranging from 7 to 3,820 m. Greatest density (27 individuals/m^2) was at depths between 25 and 49 m (Tables 11, 12; Fig. 59). Substantially lower densities (0.5 to 7.8 individuals/m^2) were found at all other depths, with density generally decreasing with increased depth. Lowest densities (0.5

to 1.5/m^2) occurred at depths greater than 500 m.

The relation between average biomass and water depth was very similar to that for numerical density, but the range in values was much more limited. Largest average biomass was 1 g/m^2 in the 25–49 m depth class. At depths greater than 500 m the biomass was very small, averaging 0.12 g/m^2 or less (Tables 13, 14; Fig. 59).

Frequency of occurrence of nemertines in samples from the eight depth classes ranged from 18 to 51% (Table 15). Higher rates of occurrence were most prevalent in the shallow-water classes, and low occurrence was typical of deepwater classes.

Relation to Sediments

Although nemertines were present in all types of sediments, they were common (13 to 28 individuals/m^2) in only two types: shell and sand (Tables 16, 17; Fig. 60). Densities of about 3 to 5 individuals/m^2 occurred in gravel, sand-silt, and silt-clay. Lower density (0.9/m^2) was found in till. Biomass of nemertines in shell bottoms was moderately large in absolute terms (6 g/m^2), but in relative terms it was exceptionally large. In all other sediments types the average biomass was 0.83 g/m^2 or less. An unusually small quantity (0.06 g/m^2) was present in till substrates (Tables 18, 19; Fig. 60).

The percentage of samples within each sediment type in which nemertines occurred was in close agreement with the quantity present. Samples from shell bottoms had the highest incidence of nemertines (50%), till the lowest (14%); their incidence in other sediment types was intermediate (28 to 47%) (Table 20).

Relation to Water Temperature

The average density of nemertines ranged from 2.4 to 25.3 individuals/m^2 throughout the entire temperature range of the study area (Tables 21, 22; Fig. 61). The highest density occurred in areas with an intermediate annual temperature range of 12° to 15.9°C. In areas where the range was either greater or less than this, the densities were substantially lower. Where the range was greater (16° to 23.9°C) density values decreased to 2.9/m^2. Where the range narrowed from 11.9° to 0°C, the values decreased from 9.0 to 2.4/m^2.

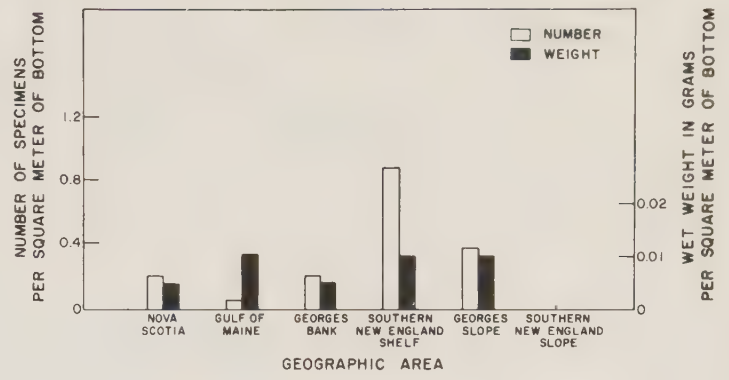


Figure 52
Density and biomass of Turbellaria in each of the six geographic areas.

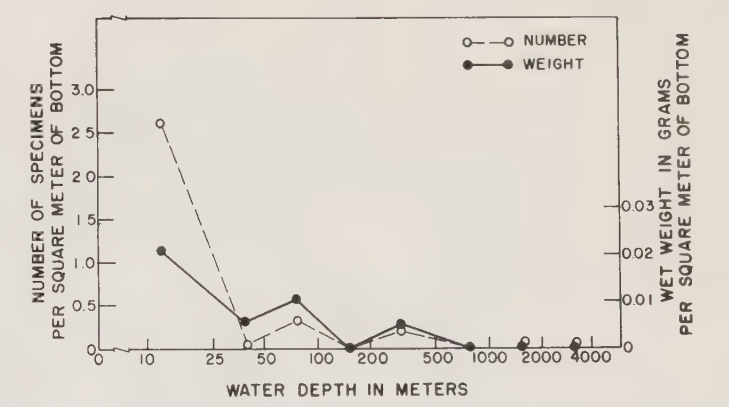


Figure 53
Density and biomass of Turbellaria in relation to water depth.

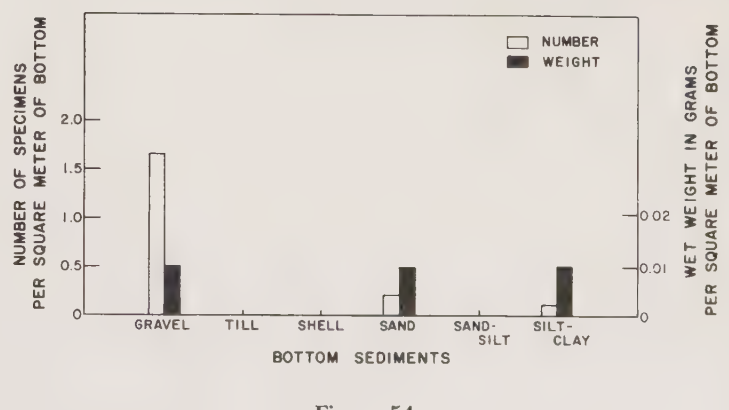


Figure 54
Density and biomass of Turbellaria in relation to bottom sediments.

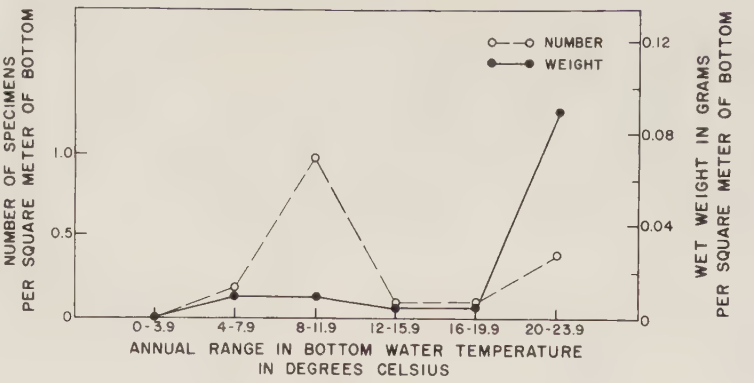


Figure 55
Density and biomass of Turbellaria in relation to the annual range of bottom water temperature.

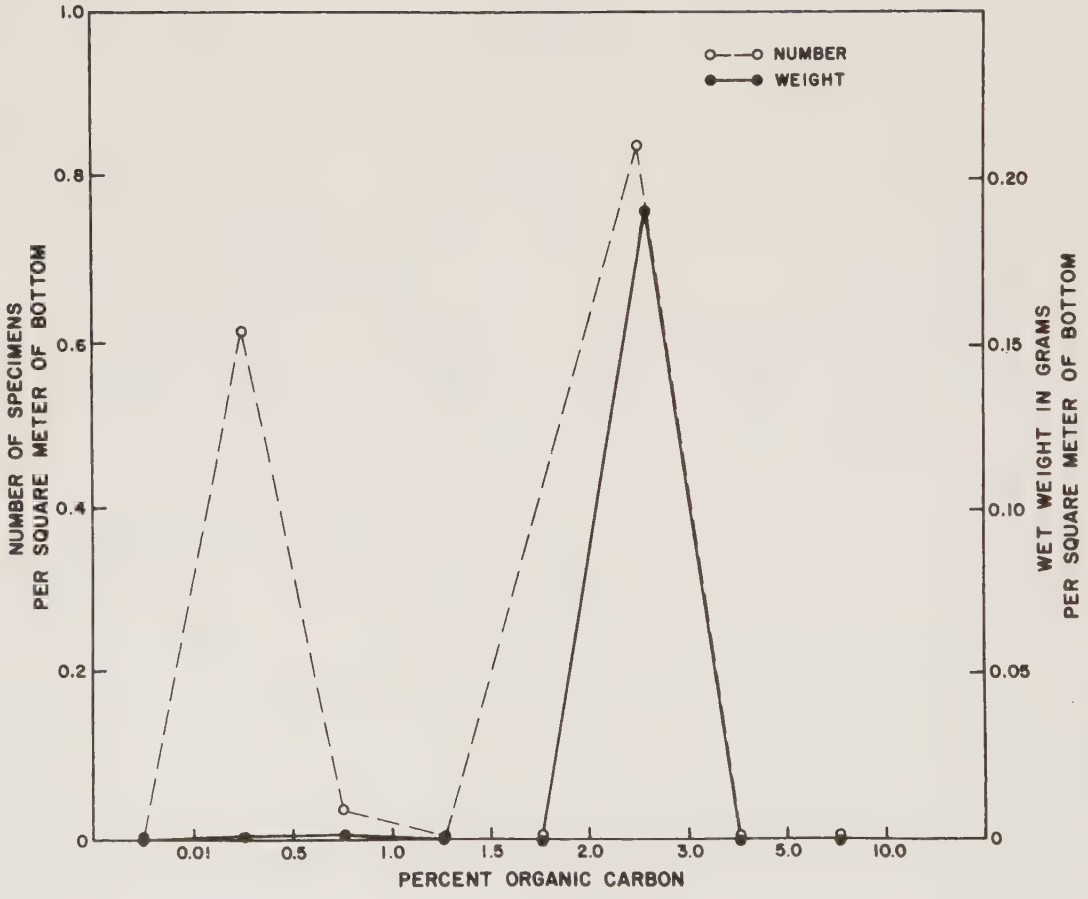
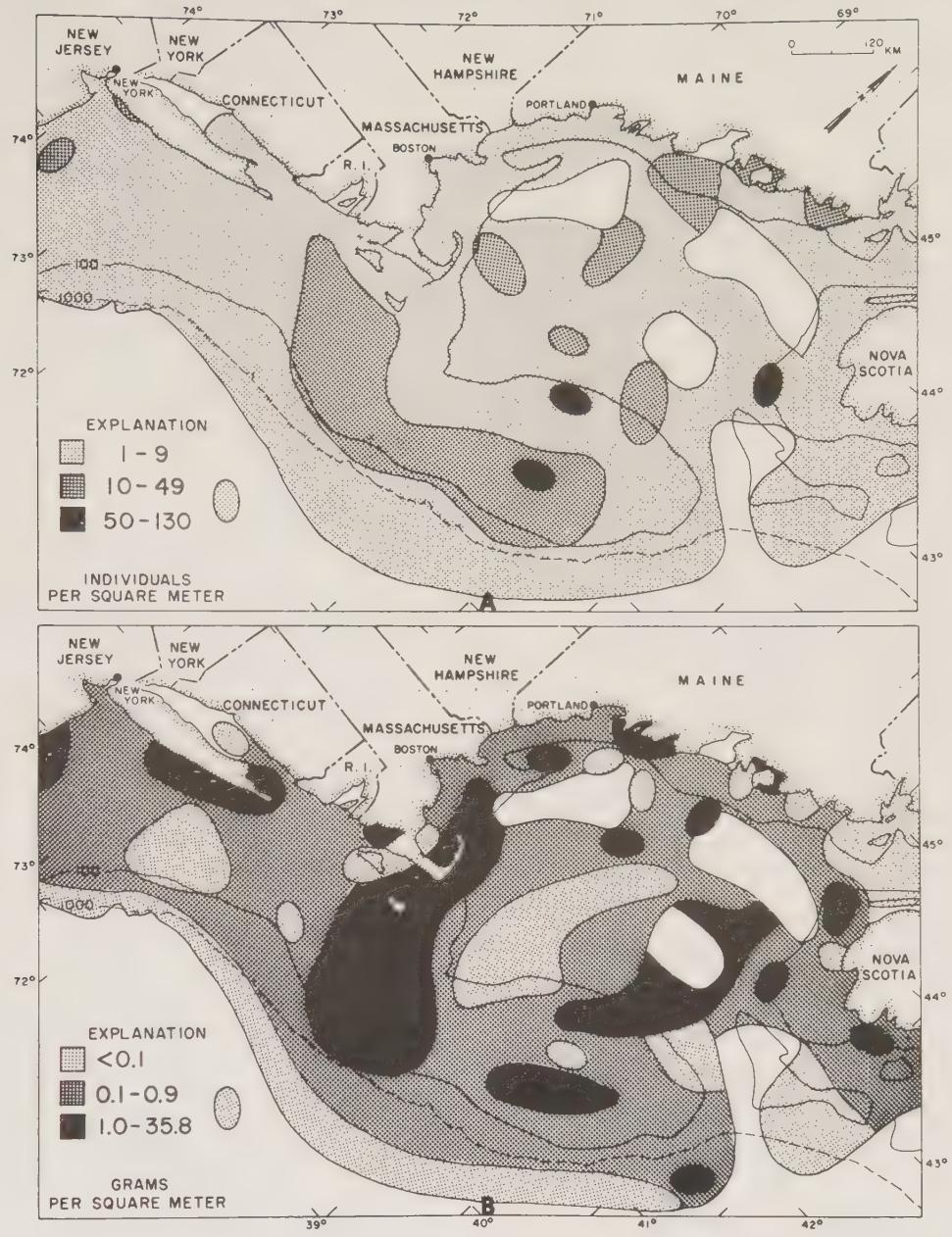


Figure 56
Density and biomass of Turbellaria in relation to sediment organic carbon.



NEMERTEA

Figure 57

Geographic distribution of Nemertea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

The relation of nemertine biomass to temperature range differed from that of density, exhibiting a general increase in biomass (from 0.22 to 1.38 g/m^2) as the temperature range broadened (Tables 23, 24; Fig. 61). Largest average biomass occurred where the range was 16° to 19.9°C, and smallest where it was less than 4°C.

The frequency of occurrence of nemertines in relation to temperature range was similar to their density distribution. The highest percentage (52 to 49%) of samples containing specimens occurred in areas with intermediate temperature ranges. Where the temperature range was narrow or broad, the frequency of occurrence was relatively low (Table 25).

Relation to Sediment Organic Carbon

The average density of nemertines exhibited a rather

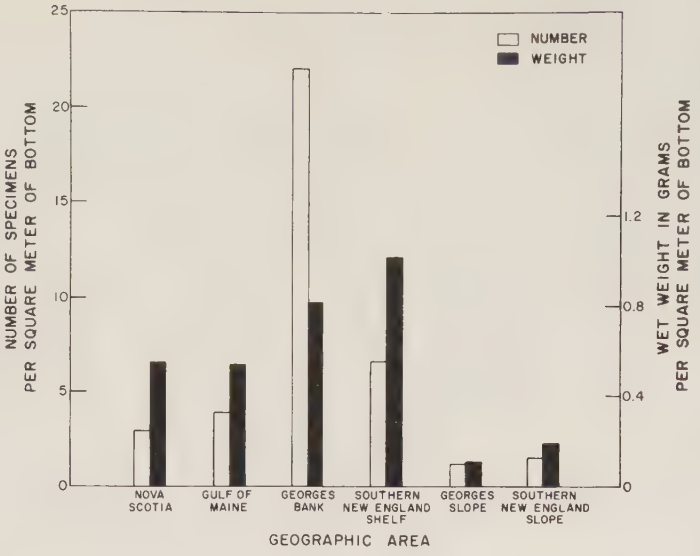


Figure 58
Density and biomass of Nemertea in each of the six geographic areas.

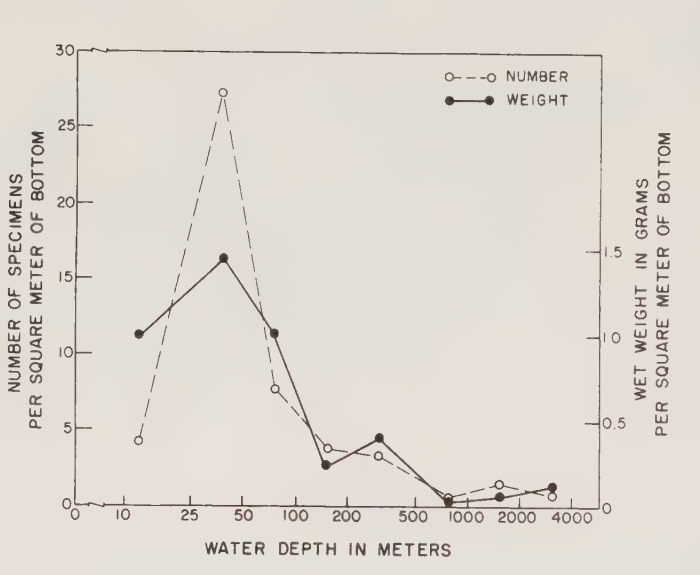


Figure 59
Density and biomass of Nemertea in relation to water depth.

sharp negative correlation to organic carbon content (Tables 26, 27; Fig. 62). Density was highest ($11/m^2$) in areas with extremely little or no organic carbon in the sediment and declined steadily (from 11 to $2/m^2$) as organic carbon content increased. None were found where carbon content exceeded 3%.

The relation of nemertine biomass to organic carbon was distinctly bimodal (Tables 28, 29; Fig. 62). Largest

biomass (0.44 g/m^2) occurred where organic carbon ranged from 1.5 to 2%, declined at higher and moderately lower levels, and showed another somewhat lower peak (0.8 g/m^2) at levels between 0.01 and 1%. Intermediate biomass occurred where carbon was absent.

Frequency of occurrence of nemertines in samples also exhibited a generally negative correlation with organic carbon content (Table 30). In areas with measurable amounts of carbon (between 0.01 and 3%), occurrence diminished from 46 to 15%. In areas with no measurable amounts, occurrence was moderately high (40%).

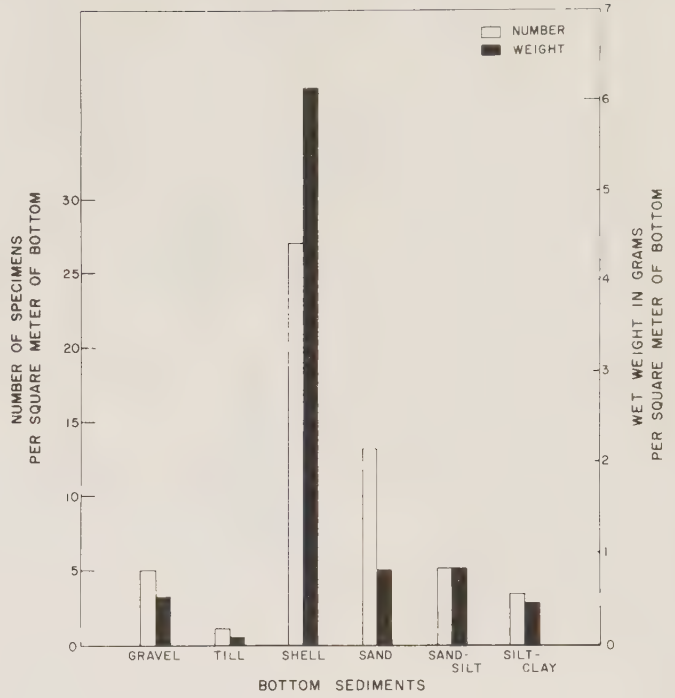


Figure 60
Density and biomass of Nemertea in relation to bottom sediments.

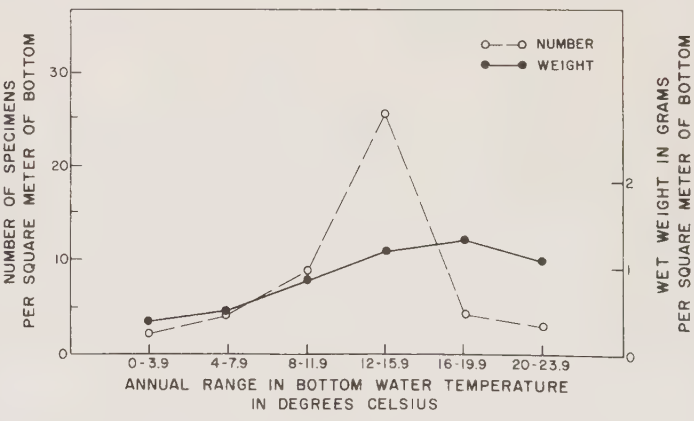


Figure 61
Density and biomass of Nemertea in relation to the annual range of bottom water temperature.

Aschelminthes

Nematoda—Free-living nematodes, members of the phylum Aschelminthes, are one of the most numerous animal groups inhabiting the bottom sediments of the northeastern coast of the United States. Previous studies conducted by Wieser (1960) in shallow coastal habitats off southeastern Massachusetts revealed nematode densities of nearly 800,000 individuals/m^2. Farther offshore, on the southeastern coast of Massachusetts at a depth of 58 m, Wigley and McIntyre (1964) encountered nematodes in densities of nearly 1 million individuals/m^2, and this measure did not include the young stages of numerous species. The vast majority of free-living nematodes are very small, less than 1 or 2 mm in length; consequently only a small portion (the large specimens) of the total population was recovered and treated in the present study. The bulk of the captured specimens were between 0.5 and 2 cm long; however, a small proportion of both larger and smaller specimens was represented. In addition to their great numerical density, this group of animals is also exceedingly profuse in species composition.

Three types of feeding habits are commonly found among free-living nematodes. Some are saprophagous, feeding on detritus and dead and decaying animal material; others are herbivorous, feeding on green plants, particularly diatoms; still others are carnivorous, ingesting rotifers, tardigrades, small annelids, other nematodes, and bryozoans.

Because of the incomplete representation of this group, the quantitative distribution discussed herein refers only to the exceptionally large species.

We found nematodes in 98 samples (9% of total); their density averaged 2.8/m^2, and the biomass averaged 0.01 g/m^2 (Table 5).

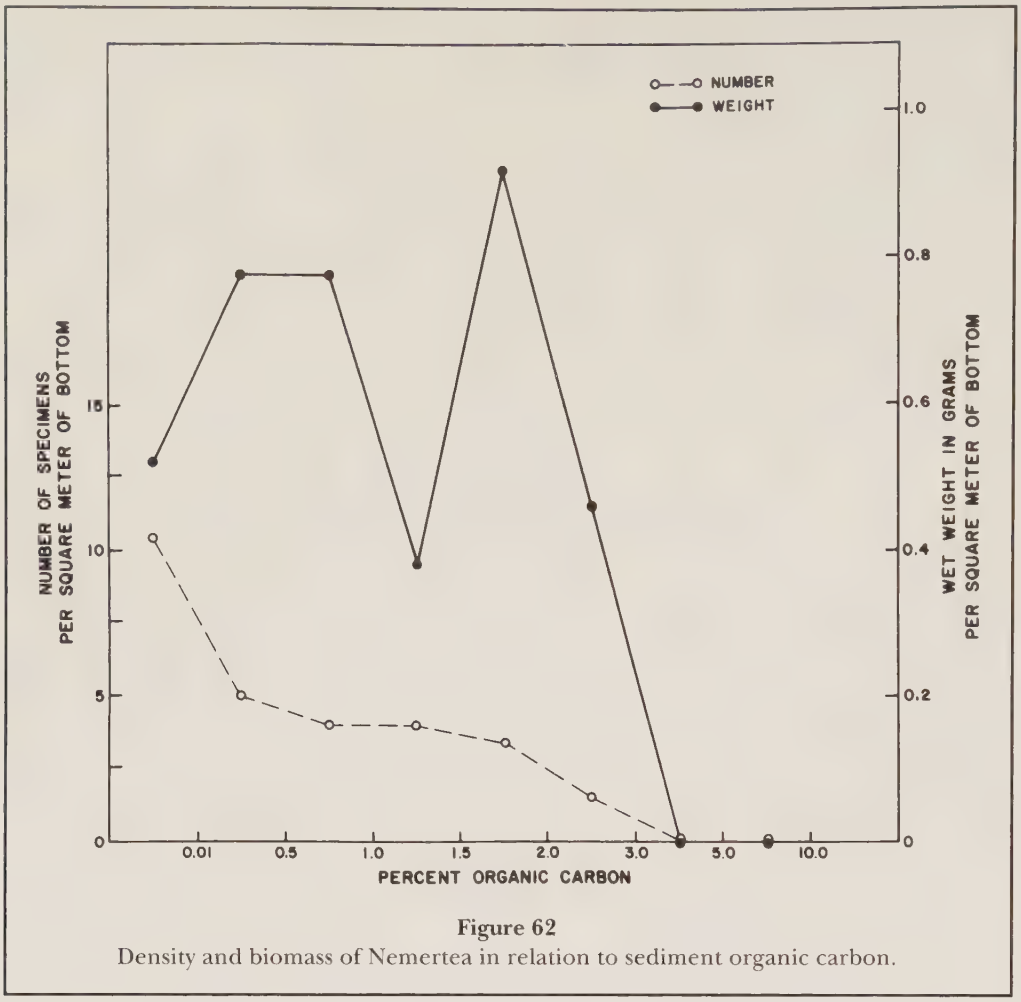


Figure 62
Density and biomass of Nemertea in relation to sediment organic carbon.

Geographic Distribution

The distribution of large free-living nematodes, although occurring in all geographic regions, was patchy (Fig. 63). They were present in coastal areas, on the offshore banks and basins, and on the continental slope and rise. They were commonly absent in samples from a number of areas: parts of the Nova Scotian shelf, large portions of the Gulf of Maine and Georges Bank, as well as many inshore bays and sounds. The pattern of their distribution suggests that they are less common in substrates where the overlying bottom current or wave action is strong, for example, the northern section of Georges Bank and at the mouth of the Bay of Fundy.

The average density of nematodes in each of the six standard geographic areas was roughly similar, ranging from 0.9 to 4.0 individuals/m^2 (Tables 6, 7; Fig. 64). Their average biomass was very low, 0.01 g/m^2 or less (Tables 8, 9; Fig. 64).

The percentage of samples containing nematodes was low (5 to 9%) in the four geographic areas on the continental shelf (Table 10), but their occurrence in the two continental slope areas was comparatively high (15 and 39%).

Bathymetric Distribution

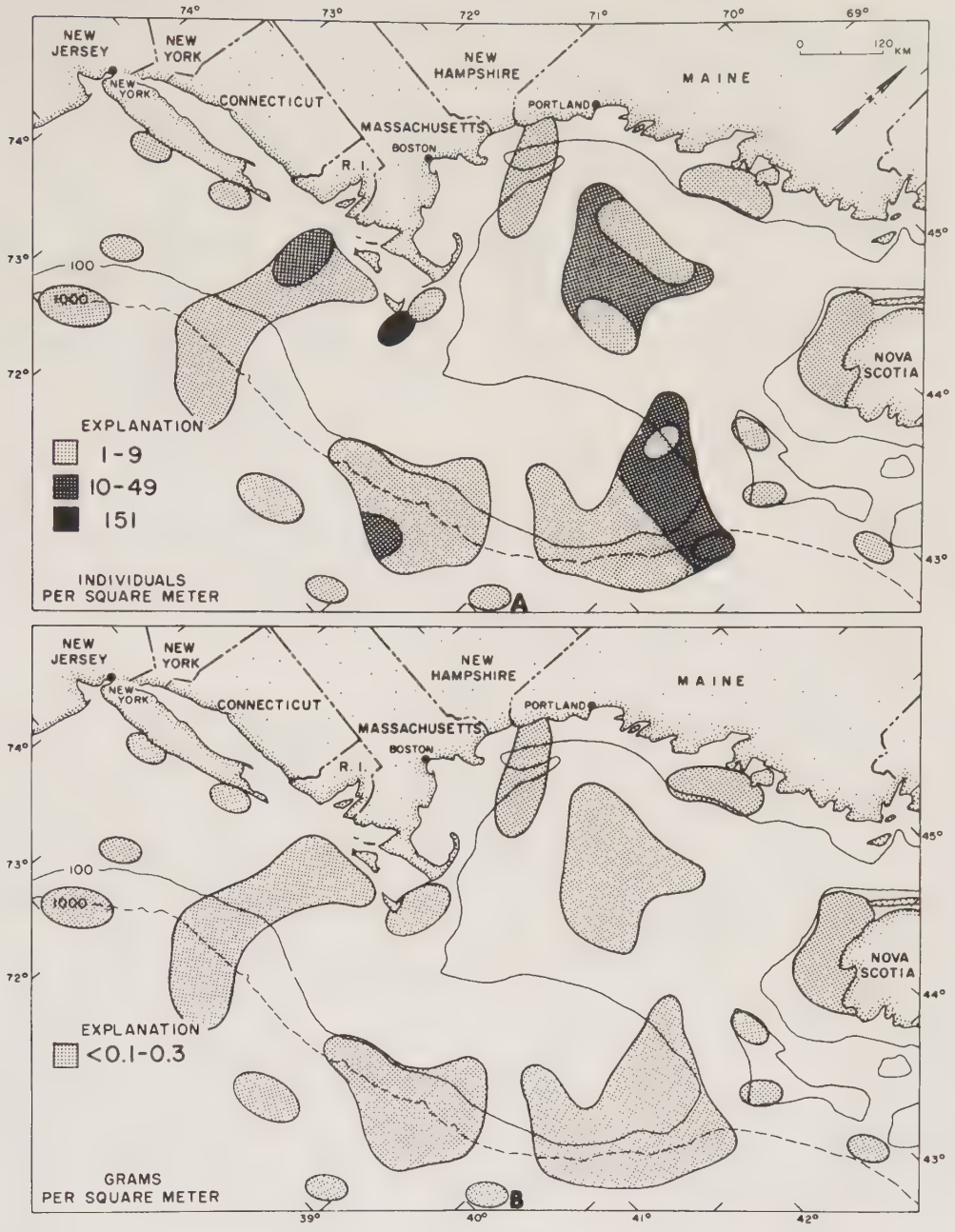
Nematodes were found at depths ranging from 23 to 3,975 m and were present in all depth classes sampled (Tables 11, 12; Fig. 65). Average density was slightly higher in the very shallow (0–24 m) and moderately deep (200–1,000) water than in other zones. Average density values ranged from 0.8 to 6.8 individuals/m^2.

Average biomass values were uniformly low (0.01 g/m^2 or less) at all depths (Tables 13, 14; Fig. 65).

Frequency of occurrence of nematodes in the samples was low (2%) in shallow water and generally increased to moderately high levels (35%) in deep water (Table 15).

Relation to Sediments

Nematodes were present in all bottom types except shell (Tables 16, 17; Fig. 66). Greatest density (8.7 individuals/m^2) occurred in gravel substrates, whereas



NEMATODA

Figure 63

Geographic distribution of Nematoda: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

all other bottom types yielded relatively moderate densities (1 to 3 individuals/m^2). Average biomass was small (0.01 g/m^2 or less) in all sediment types (Tables 18, 19; Fig. 66).

The frequency of occurrence of nematodes was moderate (12 to 13%) in gravel, sand-silt, and silt-clay but was low (4 and 5%) in sand and till (Table 20).

Relation to Water Temperature

Nematodes occurred at all temperature ranges except the highest, 20°–23.9°C (Tables 21, 22; Fig. 67). Their numerical density was greatest (2.0 to 4.3 individuals/m^2) in the narrow to intermediate temperature ranges (0°–11.9°C) and declined drastically (0.2 and 0.7/m^2) in the broader ranges.

Biomass was small, averaging only 0.01 g/m^2 or less, in all temperature ranges (Tables 23, 24; Fig. 67).

The frequency of occurrence of nematodes in samples in the various temperature ranges diminished from a high of 17%, where the temperature range was narrow, to zero where the temperature range was 20°C or more (Table 25).

Relation to Sediment Organic Carbon

Nematodes occurred only in the four low to moderate level organic carbon content classes (Tables 26, 27; Fig. 68). They were most abundant (3.1/m^2) in sediments with low organic carbon levels (0.01–0.49%) and least abundant (0.4/m^2) at moderate carbon levels (1.5–1.99%).

Biomass was very low (<0.01 to only 0.02 g/m^2) in all levels of sediment organic carbon in which they were found (Tables 28, 29; Fig. 68).

Frequency of occurrence in samples in the four carbon content classes ranged from 7 to 17% (Table 30).

Annelida

Polychaete worms formed a major component of the benthic fauna in terms of biomass and numbers of individuals. They were present throughout the study area and made up 28% of the total number of individual animals and nearly 10% of the total biomass (Table 3).

Taxonomically diverse as well as abundant, this group of organisms contributed over 300 species from among approximately 170 genera to the New England benthic fauna.

Size differential from the smallest to the largest specimen was moderate compared with that for other taxa. The smallest specimens recovered were 3 to 4 mm in length; the largest were over 200 mm. Although the vast majority of annelids from these collections are elongate and cylindrical in shape (similar to the common earthworm), the species that is largest in terms of weight is *Aphrodita hastata,* the sea mouse. It is ovate in shape, ventrally flattened, convex dorsally, and weighs 75 g or more. The average wet weight of individual annelids in the region is less than 0.05 g. A wide

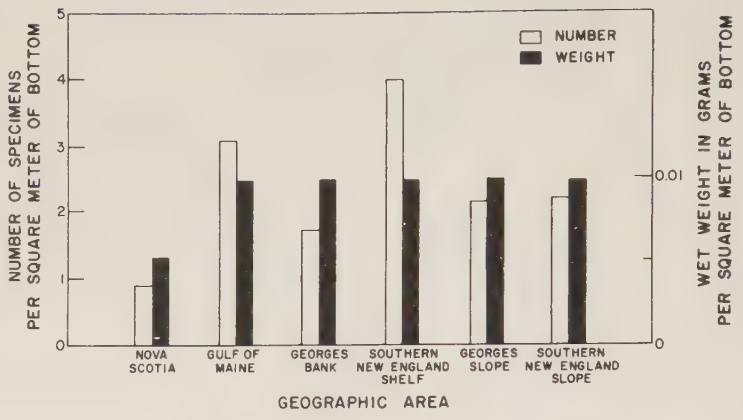


Figure 64
Density and biomass of Nematoda in each of the six geographic areas.

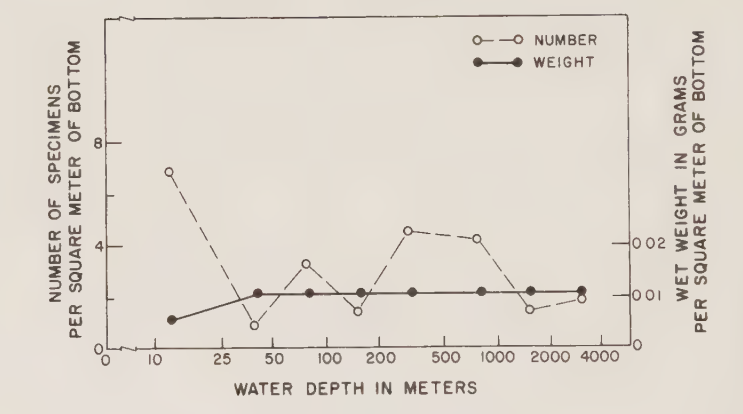


Figure 65
Density and biomass of Nematoda in relation to water depth.

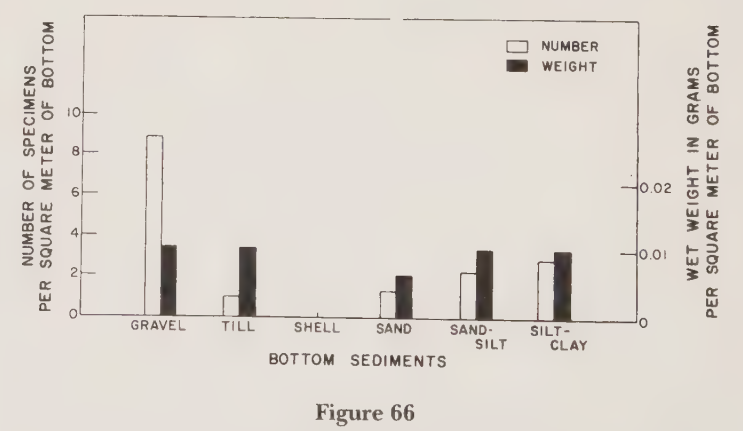


Figure 66
Density and biomass of Nematoda in relation to bottom sediments.

variety of morphologically different forms abound. All the different feeding types—carnivores, suspension feeders, and selective and nonselective deposit feeders—were represented in our samples. Many representatives from the two major life modes, the errant (or free living) and the sedentary (tubicolous) polychaetes were collected.

Coloration of polychaete annelids is extremely diverse, from nearly translucent and white to a dark brown. Predominant hues are light beige, tan, dark brown, and various shades of olive and red. Some annelids displayed a cuticular irridescence that greatly enhanced their appearance. Some forms possessed variegated pat-

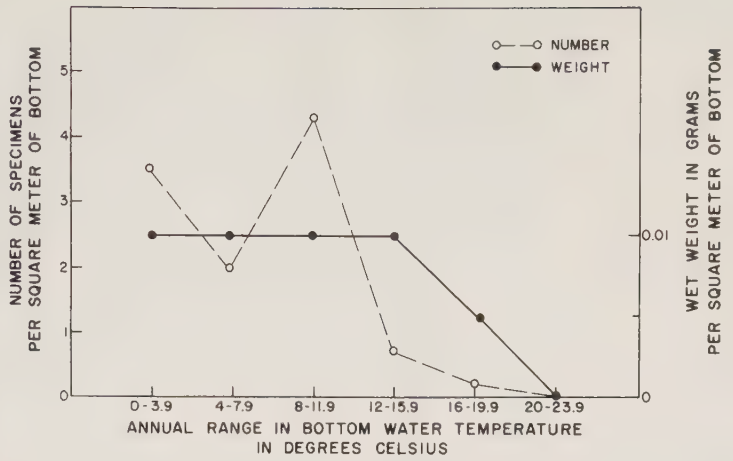


Figure 67
Density and biomass of Nematoda in relation to the annual range of bottom water temperature.

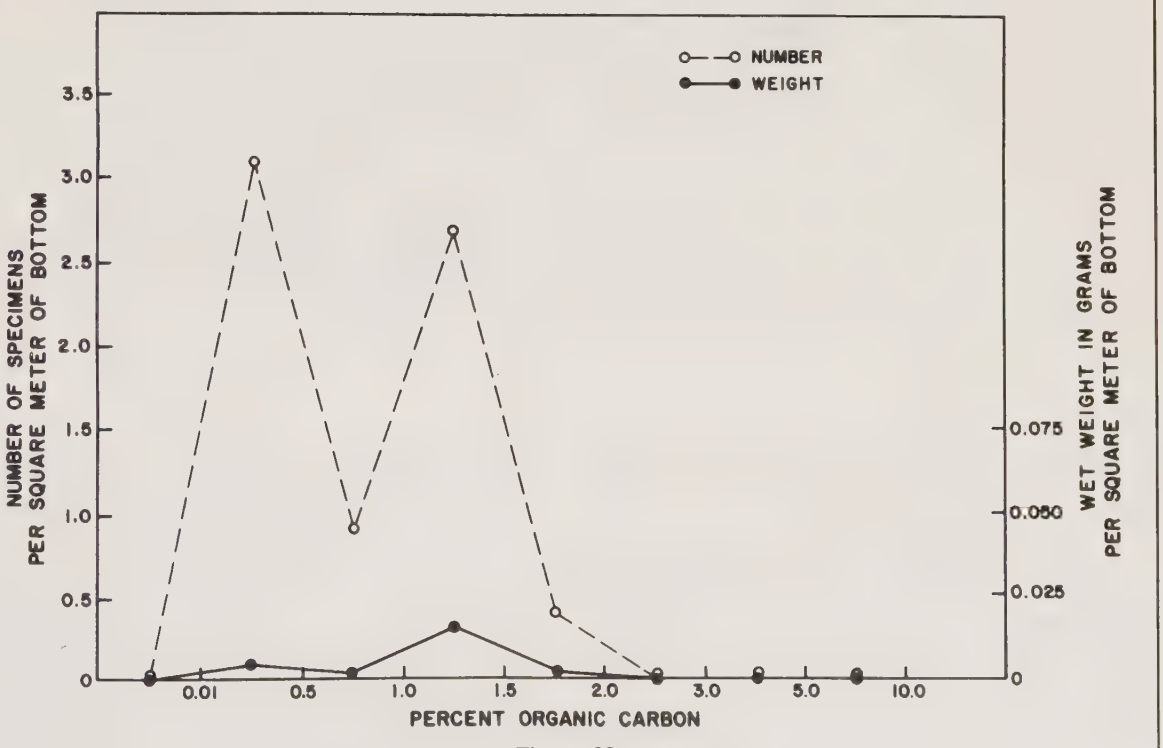
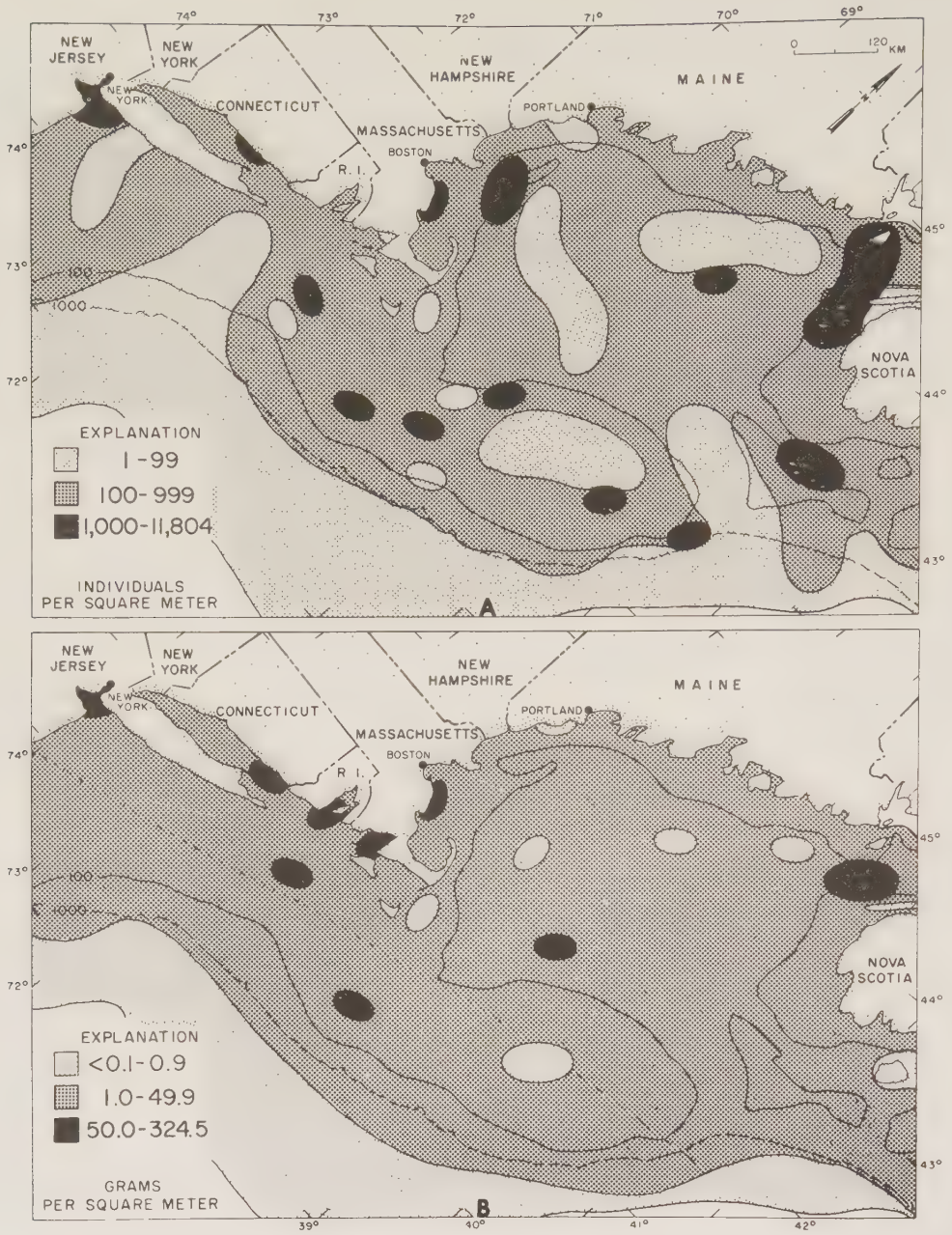


Figure 68
Density and biomass of Nematoda in relation to sediment organic carbon.



ANNELIDA

Figure 69

Geographic distribution of Annelida: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

terns of color on various parts of the body, including scarlet branching gills. Tubicolous forms, especially, exhibited a wide range of color patterns on their tentacles and branchiae.

A few species are commensal on sponges and echinoderms, but more often they themselves are the hosts to commensal partners, for example the *Chaetopterus–Pinnixa* (Decapoda) relationship and the *Clymenella–Listriella* (Amphipoda) relationship.

Annelids occurred in 1,034 samples (96% of total), their density averaged 425/m^2,and their biomass averaged 17.4 g/m^2 (Table 5).

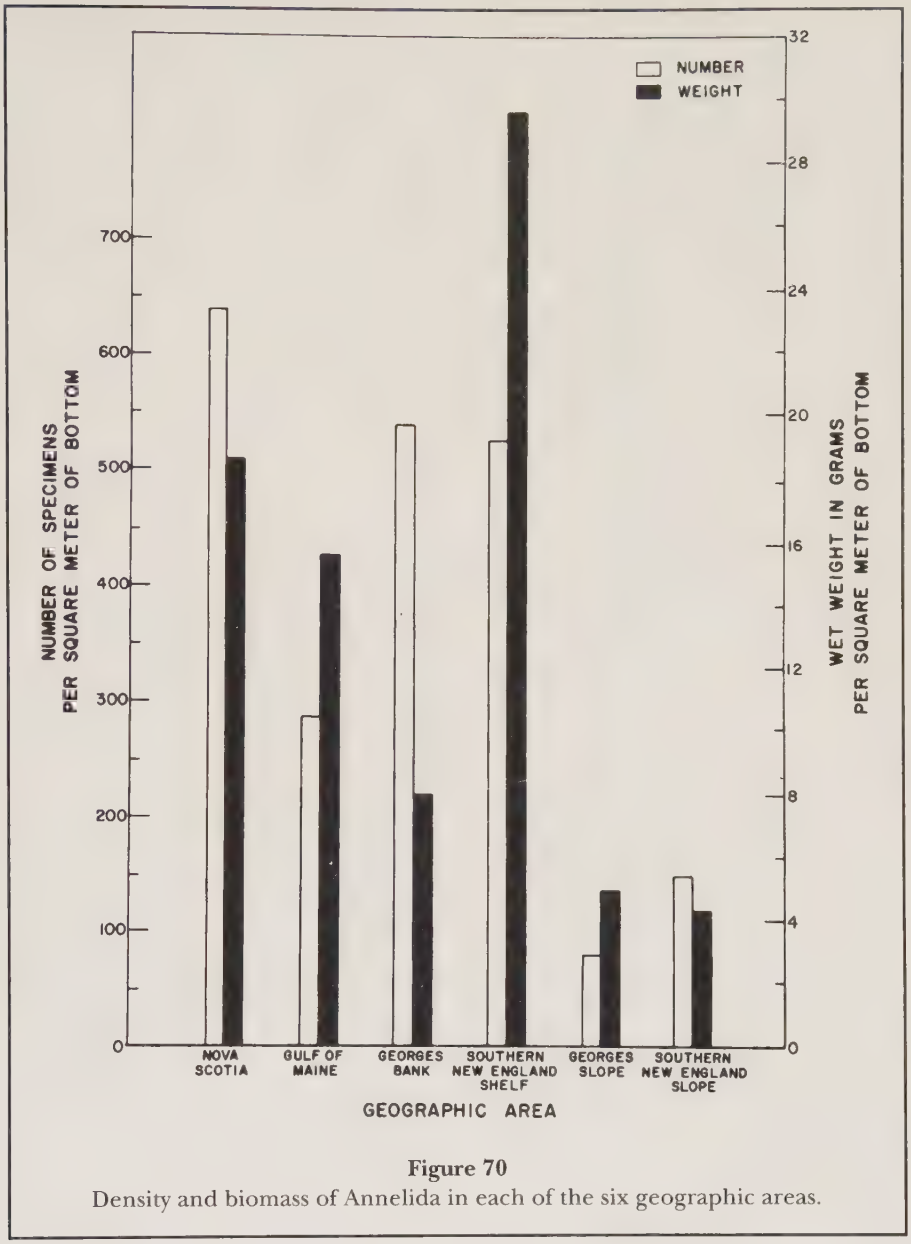


Figure 70
Density and biomass of Annelida in each of the six geographic areas.

Geographic Distribution

Annelid worms were found in all parts of the study area (Fig. 69). Only the Mollusca, Crustacea, and Echinodermata compare with their widespread distribution, and only the Crustacea are more numerous.

The density of annelids on the continental shelf and slope generally averaged between 100 and 1,000 individuals/m^2. Over approximately 10% of the shelf and slope area, the density of annelids was high, 1,000 to 12,000/m^2. About 30% of the shelf and slope area yielded less than 100/m^2. In deepwater regions beyond the continental slope, the density was relatively low, usually less than 100/m^2.

The biomass of annelid worms on the continental shelf and slope, with few exceptions, averaged between 1 and 50 g/m^2 and reached a maximum of 325 gm^2. Among the six standard geographic areas, two slope areas (Georges Slope and Southern New England Slope) had the lowest numerical density and smallest biomass of annelids, 80 to 149 individuals/m^2 and about 4 to 5 g/m^2 (Tables 6–9; Fig. 70).

In the four continental shelf areas the numerical density of annelid worms was high. Average densities ranged from 291 to 648 individuals/m^2 and greatest density was in the Nova Scotia area. Biomass in these areas, also, was moderately high; average values ranged from 8 to 30 g/

m^2. Largest average biomass occurred in the Southern New England Shelf area (Tables 6, 8).

The percentage of the total fauna made up by annelids was high in both biomass and number of individuals (Tables 7, 10). On a numerical basis, annelids accounted for 22 to 56% of the total fauna. In terms of biomass, annelids formed between 3 and 23% of the total fauna. In the two deepwater zones, Georges Slope and Southern New England Slope, the percentage of the total biomass made up by annelids was 22 and 23%, respectively. This is an especially large proportion to be formed by any one faunal group and a much higher proportion than that from the continental shelf areas where the percentages were only 3 to 12.

Annelid worms were present in an exceptionally large proportion of the samples. In all standard geographic areas, except Georges Bank, they were present in 96 to 99% of the samples. On Georges Bank they were present in 89% of the samples (Table 10).

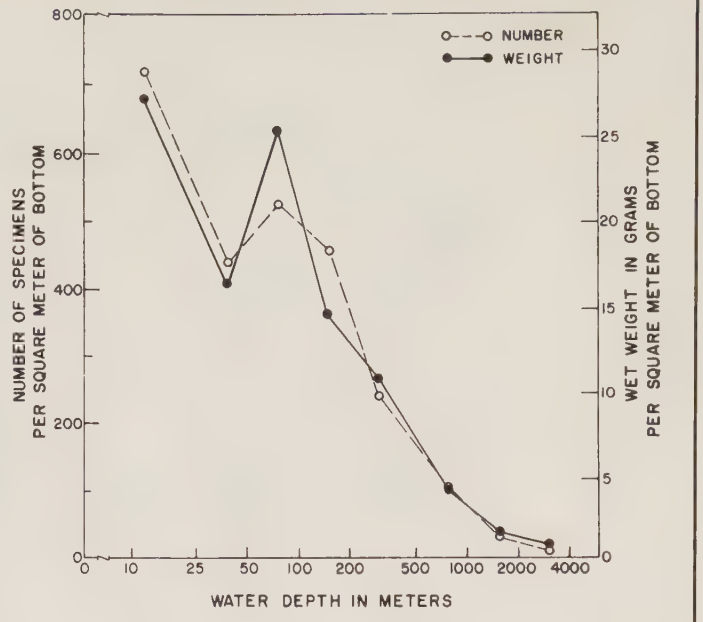


Figure 71
Density and biomass of Annelida in relation to water depth.

Bathymetric Distribution

Annelids occurred over the entire depth range in which samples were collected, 3 to 3,975 m. Numerical density and biomass were highest in shallow water and decreased in quantity rather uniformly with increased water depth (Fig. 71). Average density in the shallowest depth class was 719 individuals/m^2. High densities (437 to 159/m^2) prevailed across the continental shelf and then diminished rather sharply down the slope and on the continental rise, where the average density was only 9/m^2 (Tables 11, 12).

The biomass of annelids followed precisely the same quantitative trend in relation to water depth as was exhibited by numerical density. Average biomass was largest (27 g/m^2) in the shallowest depth zone. Biomass was rather high (15 to 25 g/m^2) on the continental shelf and dropped to 5 g/m^2 at midslope and to 0.76 g/m^2 on the continental rise (Tables 13, 14).

Annelids were present in a very high percentage of the samples from all depth classes. Frequency of occurrence among the eight classes ranged from 93 to 100% (Table 15).

Relation to Sediments

Annelid worms were not only present in all sediment types sampled but occurred in roughly the same density in each of the different sediment types (Tables 16, 17; Fig. 72). Average density from all sediment types ranged from 232 to 558 individuals/m^2. Greatest densities were found in sand and gravel bottoms, lowest densities in silt-clay and till.

Biomass, also, was rather evenly distributed among the various sediment types. Values ranged from 11 to 26 g/m^2. Highest average biomass occurred in sand-silt sediments, and the lowest occurred in till. Intermediate and nearly equal quantities, 15 to 16 g/m^2, were present in the other four bottom types (gravel, shell, sand, and silt-clay) (Tables 18, 19; Fig. 72).

Annelid worms were present in all samples from till, shell, and sand-silt sediments; however in 97% of samples in gravel and silt-clay. Although annelids were present in 94% of the samples from sand sediments, this category of bottom type ranked last in this relationship (Table 20).

Relation to Water Temperature

Annelids were present in greatest quantities (Table 21; Fig. 73) where the annual range in bottom water temperature was broadest, and densities generally declined as the temperature range decreased. Where the temperature range was greater than 20°C, average density of annelids was 1,698 individuals/m^2. At the other extreme, where the temperature range was less than 4°C, average density was 212/m^2. At intermediate levels of temperature range, density was intermediate, 280 to 568 individuals/m^2. The percentage composition of numbers in this group of organisms in relation to the total fauna in the various temperature-range classes varied from 16 to 49% (Table 22). Percentages were highest where temperature ranges were extremely high and low.

Biomass of annelids in relation to range of water temperature was similar to that for density. Biomass was large (about 40 g/m^2), not only in relative terms but in absolute quantities, in areas where the temperature range was broad

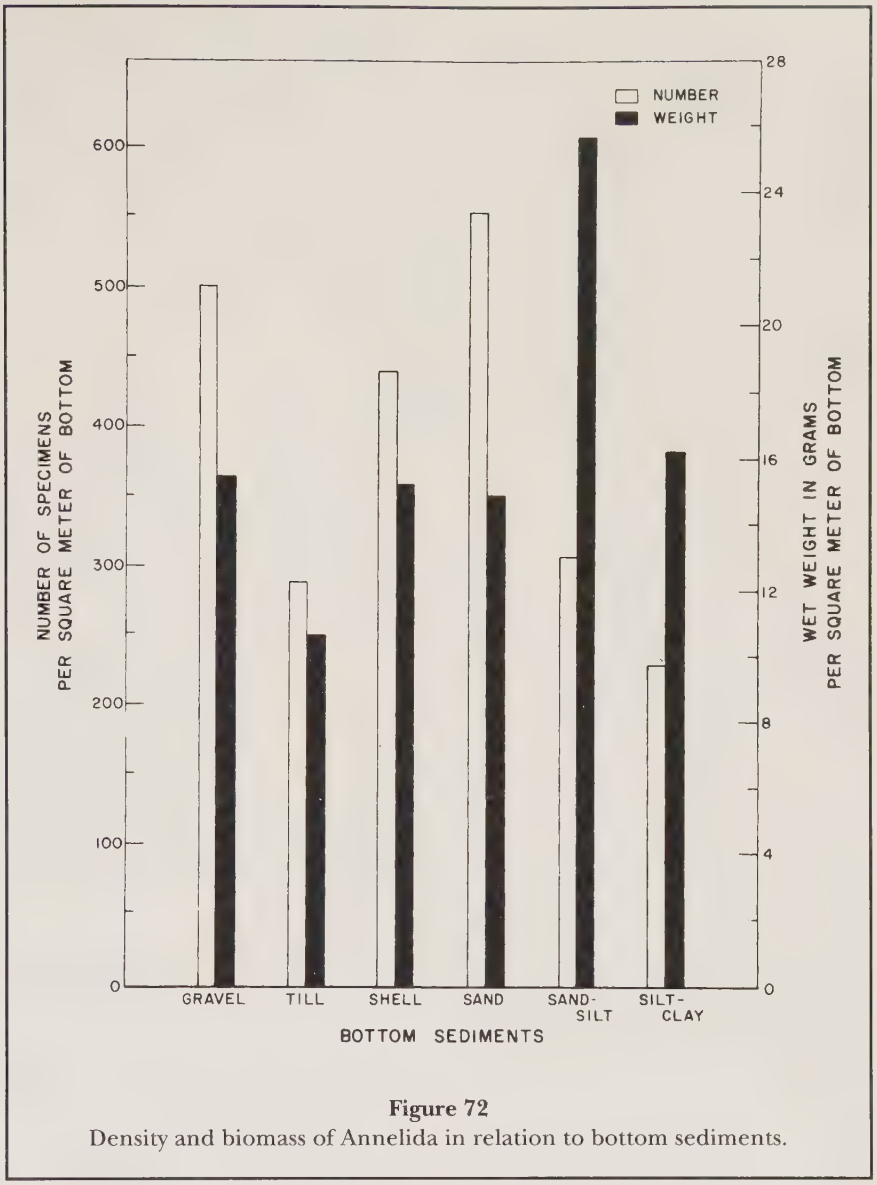


Figure 72
Density and biomass of Annelida in relation to bottom sediments.

(Tables 23, 24; Fig. 73). Conversely, quantities were smaller (about 10 g/m^2) where the temperature range was small. Moderate biomasses were encountered in areas where the temperature range was moderate.

The frequency of occurrence of annelids among the temperature-range classes was high and fairly uniform. They occurred in 92 to 97% of the samples (Table 25).

Relation to Sediment Organic Carbon

Annelids of the New England region exhibited an essentially bimodal relationship to the amount of organic carbon in the sediments (Fig. 74). Greatest density (504/m^2) occurred at low organic carbon levels (between 0.01 and 0.49%); another peak in density (407/m^2) occurred at higher levels (between 2 and 3%); moderate densities prevailed at levels between these two peaks, with smallest densities occurring in both lowest and highest levels (0.00 and 5.00+%) of sediment organic carbon (Tables 26, 27).

Annelid biomass was greatest (27 g/m^2) at organic carbon levels between 1.5 and 2% (Tables 28, 29; Fig. 74) and gradually diminished at levels both above and below these values. As with density, lowest biomass was found in both the lowest (0.00%) and highest (5.00+%) organic carbon levels.

Frequency of occurrence of annelids in the various organic carbon content classes was uniformly high, ranging from 80 to 100% in all classes except one, the 3–5% class, in which only 50% of the samples contained members of this group (Table 30).

Pogonophora

Pogonophora (beard worms) are a minor consituent of the New England benthos. They provided less than 0.1% of the total number of specimens and biomass of organisms in the study area (Table 3). Nevertheless, they contributed some unique records to the study. Chief among them was a proclivity for deep, cold water. These unusual animals were one of only a few taxonomic groups that were more abundant in deep water than in shallow water.

Pogonophores inhabit chitinous tubes buried in the bottom sediments. The tubes in our collections ranged in length from about 5 to 15 cm and had diameters from 0.1 to 0.4 mm. The colors of the tubes varied from very light tan to dark brown, but were most frequently of a greenish-yellow to brownish-green hue. The majority of them exhibited alternating light and dark rings or bands. Embryos were not uncommon in the tubes from our samples. Preserved specimens varied in color from whitish to brown; the most common colors observed were cream to light reddish tan.

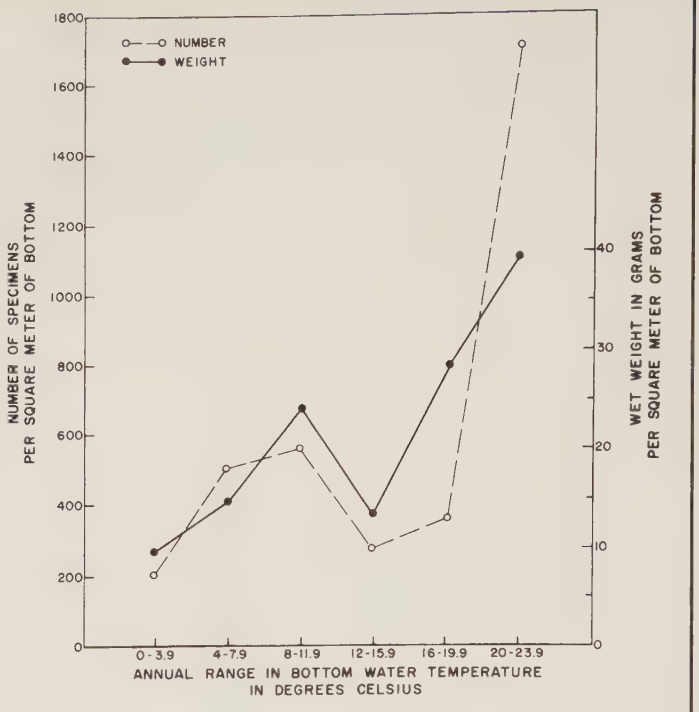


Figure 73
Density and biomass of Annelida in relation to the annual range of bottom water temperature.

The two existing orders of pogonophores, the Athecanephria and Thecanephria, are represented in our collections by species from the genera *Siboglinum*, in the former, and *Diplobranchia* and *Crassibrachia*, in the latter. Six species were obtained; the most common were *Siboglinum ekmani* Jagersten, *S. pholidotum* Southward and Brattegard, and *Diplobrachia similis* Southward and Brattegard. Less common were *Siboglinum holmei* Southward, *S. angustum* Southward and Brattegard, and *Crassibrachia sandersi* Southward. *Siboglinum holmei* was distinctive for its occurrence in the Gulf of Maine and was the only species of this phylum found in the Gulf. Furthermore, it was taken in close proximity to land, at the point nearest land, at station 1171, less than 5 km from Grand Manan Island and 10 km from the mainland coast of the U.S. Water depth at this location is 141 m.

Pogonophora occurred in 56 samples (5% of total); their density averaged 0.6/m^2 and their biomass averaged less than 0.01 g/m^2 (Table 5).

Geographic Distribution

Pogonophores were widely distributed along the continental slope and continental rise from New Jersey northward to Nova Scotia but rarely occurred on the continental shelf (Fig. 75). In coastal waters they were encountered in only the most northerly part of the study area, near Grand Manan Island (New Brunswick), Canada, and Eastport, Maine. Their average density throughout the study area was low or moderately low, between 1 and 51/m^2. Because of their small size and low density the average biomass of pogonophores was very small, less than 0.2 g/m^2 in all localities sampled.

Among the six standard geographic areas, pogonophores were present in significant quantities only in the Georges Slope and Southern New England Slope areas (Tables 6–9; Fig. 76) where density in those two areas averaged 3 and 5/m^2, respectively, and biomass 0.01 and 0.03 g/m^2, respectively.

In view of the relatively recent date (Ivanov, 1963) this phylum was first reported from the New England Region, the frequency of occurrence in this series of samples should be considered unexpectedly high. Pogonophores occurred in 35% of the samples from Georges Slope and in 42% of the Southern New England Slope samples (Table 10). In two other geographic areas they were present in 2% or less of the samples. They were absent in the Georges Bank and Southern New England Shelf areas.

Bathymetric Distribution

Pogonophores were found at depths from 141 to 2,870 m. Not only were members of this phylum restricted to deep water, but their density, biomass, and frequency of occurrence were higher in the middle and deeper portions of their range than in shallow parts (Fig. 77).

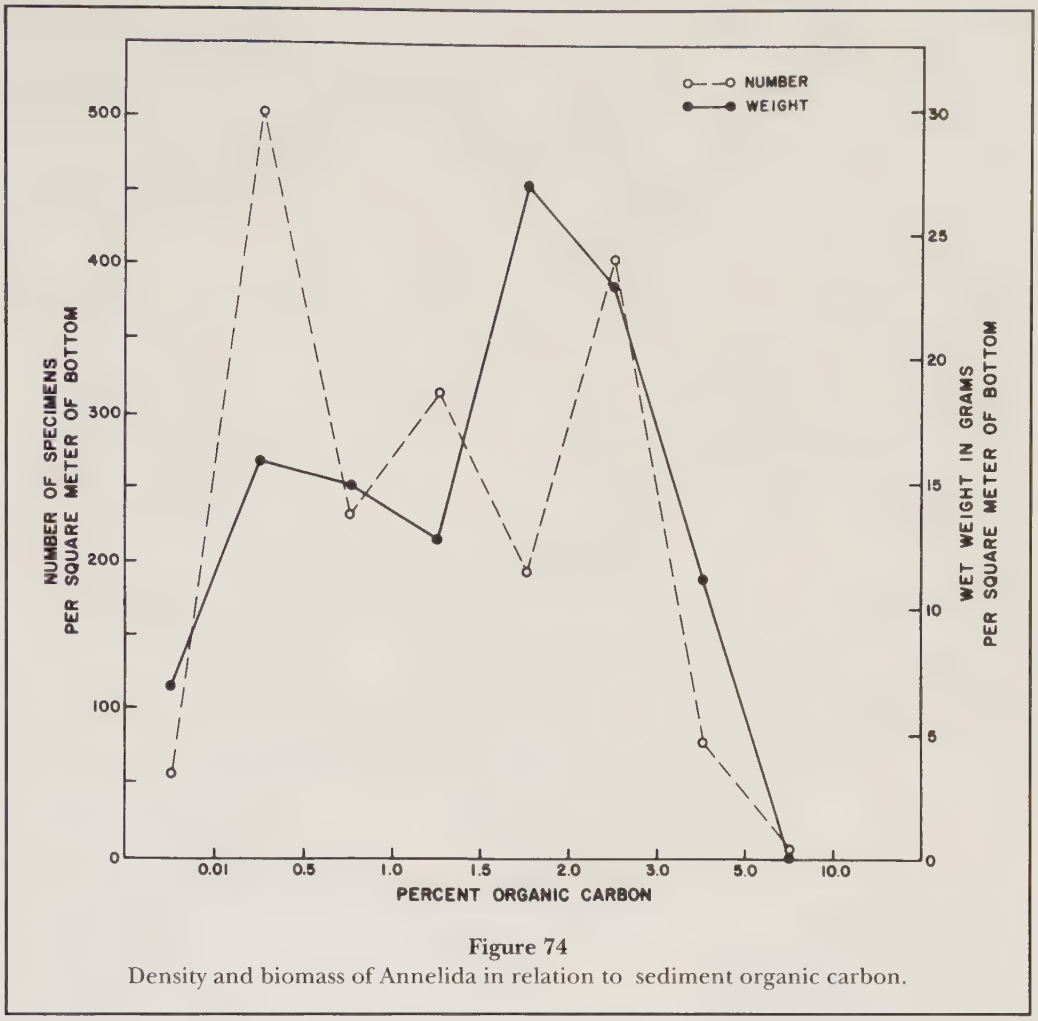


Figure 74
Density and biomass of Annelida in relation to sediment organic carbon.

Average density was highest (6.8 individuals/m^2) between 500 and 1,000 m. Density was slightly lower (3.2 to 3.5/m^2) in deeper water (1,000 to 2,870 m) but substantially lower in depths less than 500 m (Table 11).

Biomass ranged from 0 to 0.03 g/m^2, and the trend in relation to water depth was comparable to that described for density (Table 13).

Pogonophores were present in approximately half the samples from depths greater than 500 m. In the two shallower but adjacent depth classes (100–199 m and 200–499 m), there was a sharp drop in their occurrence to 5 and 1%, respectively, They were absent in the three shallow depth classes (Table 15).

Relation to Sediments

Pogonophorés were absent in coarse textured sediments but were increasingly common as the sediment particle size decreased from sand to silt-clay (Fig. 78). The density of pogonophores was exceedingly sparse (<0.1/m^2) in sand sediments, intermediate in sand-silt, and highest (1.9/m^2) in silt-clay (Table 16).

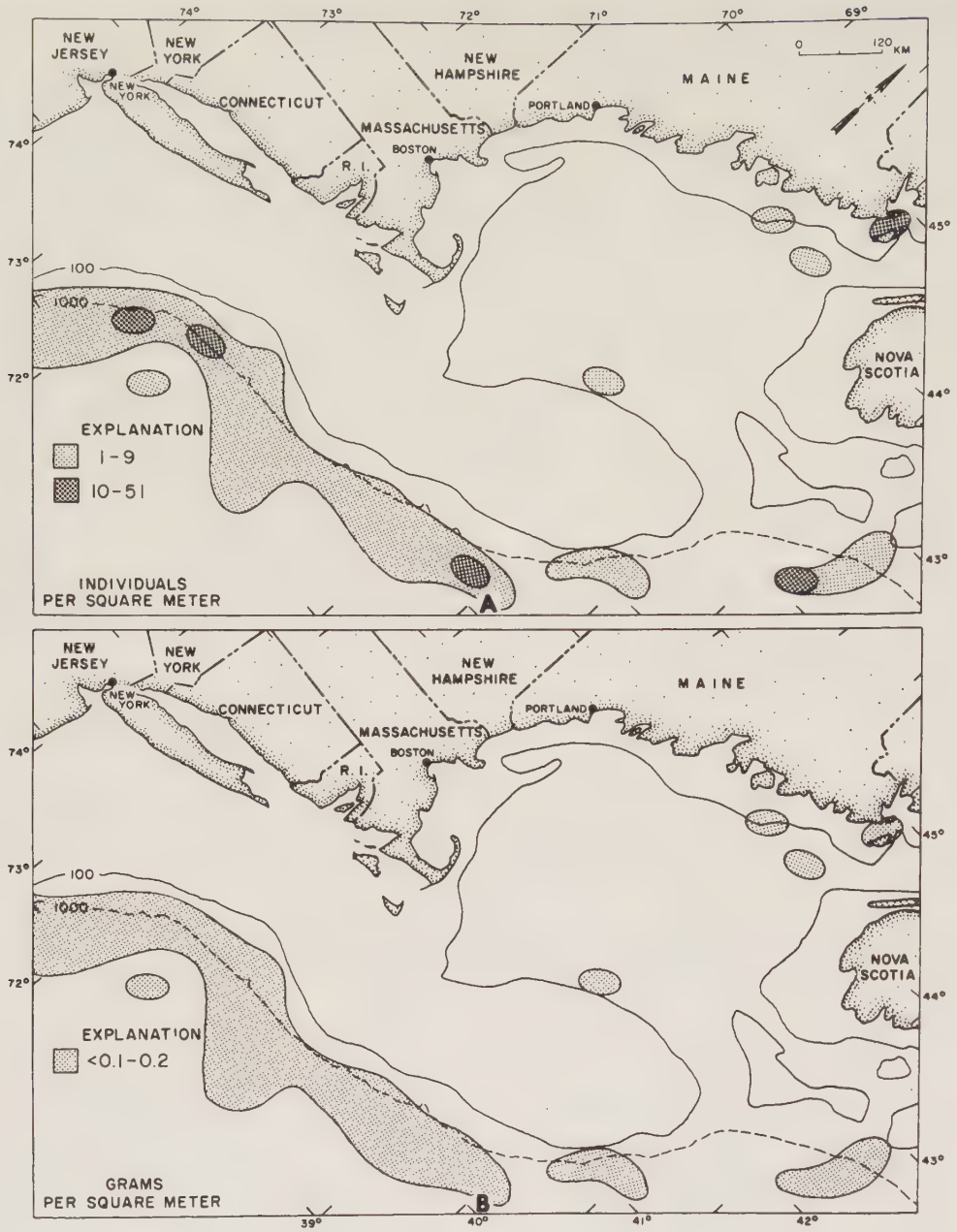
Their biomass was very low (<0.01 g/m^2) in sand, and only slightly higher in the other fine-grade sediments (Table 18).

The occurrence of pogonophores in the samples correlated very closely with average density. They were exceedingly sparse (occurring in <1%) in samples from sand sediments, moderately sparse in sand-silt, and most common (16%) in silt-clay substrates (Table 20).

Relation to Water Temperature

Pogonophores were restricted in their distribution to areas that exhibited an annual bottom temperature range of less than 12°C (Fig. 79). The vast majority were obtained where the temperature range varied less than 4°C. In these waters their density averaged 1.5/m^2 and the biomass averaged 0.01 g/m^2 (Tables 21, 23). Even in areas where the temperature range was between 4° and 11.9°C they were exceedingly sparse in both density (0.1 and 0.7/m^2) and biomass (<0.01 g/m^2).

The areas of small temperature variation (see Fig. 11) correspond to the deepwater regions on the conti-



POGONOPHORA

Figure 75

Geographic distribution of Pogonophora: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

nental slope and continental rise (see preceding sections on geographic and bathymetric distribution).

Among the three temperature range classes in which pogonophores were found, their frequency of occurrence was highest (15% of the samples) where the temperature range was smallest. Frequency of occurrence was very low in the other two temperature range classes in which they occurred.

Relation to Sediment Organic Carbon

Pogonophores were found where sediment organic carbon content was low to moderate, ranging from 0.01 to slightly under 2% (Fig. 80).

Highest density ($2.2/m^2$) occurred in carbon contents in the 0.50 to 0.99% range, and lowest ($0.1/m^2$) in the 1.50 to 1.99% range (Table 26).

Biomass was low (0.01 to <0.01 g/m^2) in the four organic carbon range classes in which they occurred (Table 28).

The greatest frequency of occurrence (21%) in samples was in the 0.50 to 0.99% range class, but frequency diminished rapidly in the higher and lower adjacent classes (Table 30).

Sipunculida

Sipunculids, or peanut worms as they are sometimes called, are a taxonomically small group but are found in great abundance in some habitats and have a wide distribution in many parts of the world ocean. Although locally abundant in New England waters, they account for less than 0.5% of the total benthic fauna in terms of both numerical density and biomass (Table 3).

Peanut worms are elongate and cylindrical in shape and characteristically burrow into the bottom sediments where they feed predominantly on detritus. A few species utilize abandoned gastropod shells for permanent shelter, and one small species was found to inhabit empty foraminifera tests.

Specimens in our samples ranged in length from about 0.5 to 12 cm.

Brown, in various shades, was the predominant color exhibited by our specimens; most often they were tan, flesh, or reddish-brown.

Sipunculids occurred in 249 samples (23% of total). Their density averaged 5.9/m^2, and biomass averaged 0.75 g/m^2 (Table 5).

Geographic Distribution

Sipunculids were widely distributed over the study area (Fig. 81), occurring in low densities over large areas of banks and basins. Densities generally averaged between 1 and 49 individuals/m^2 and exceeded these values in only three localities. The maximum density detected was 152 individuals/m^2.

Average biomass of sipunculids was moderately low, usually 1 g or less per square meter, and with few exceptions was less than 10 g/m^2.

Among the six standard geographic areas there was rather little difference in average density (Table 6; Fig. 82); the range was about 1 to 9 individuals/m^2. Slightly

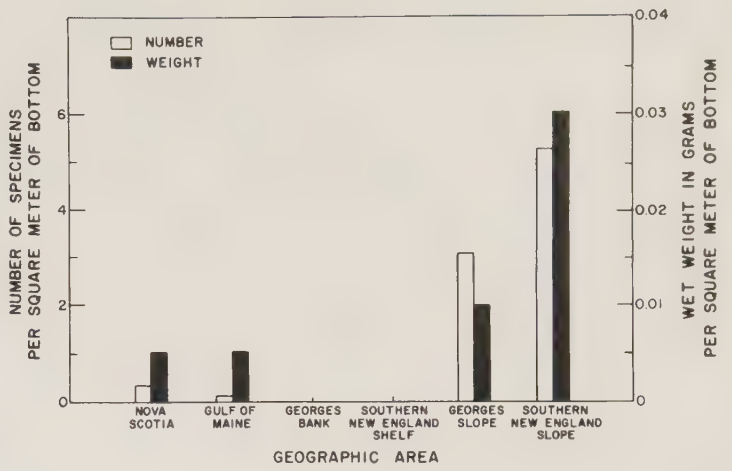


Figure 76
Density and biomass of Pogonophora in each of the six geographic areas.

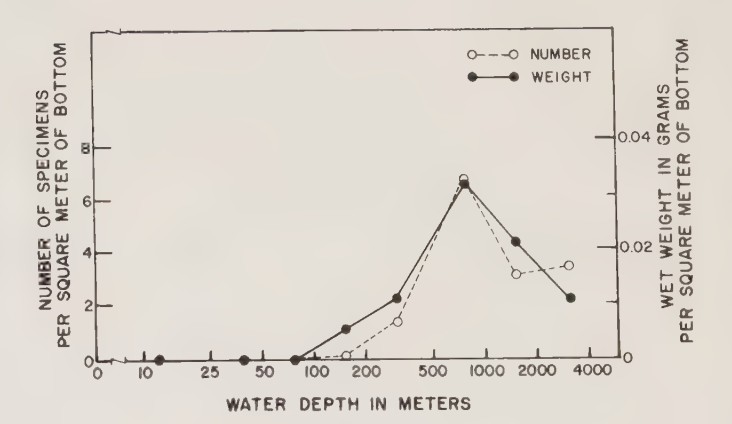


Figure 77
Density and biomass of Pogonophora in relation to water depth.

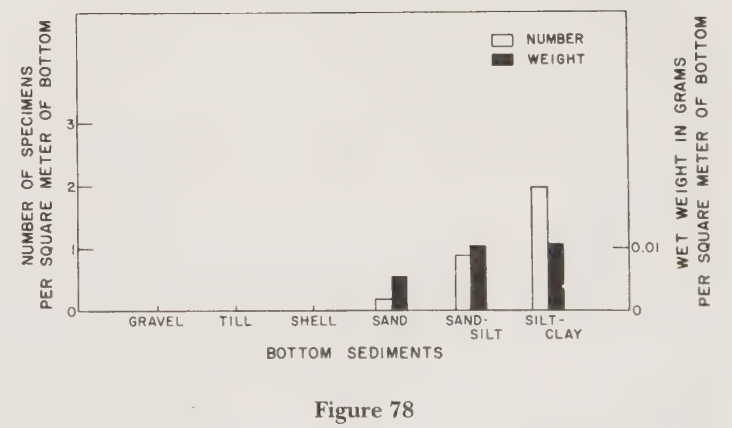


Figure 78
Density and biomass of Pogonophora in relation to bottom sediments.

higher average densities were found in Nova Scotia, Southern New England, and the Southern New England Slope. The lowest density (1.2/m^2) was in the Georges Slope area.

Differences in average biomass were also comparatively small among the six geographic areas (Table 8; Fig. 82). Largest average biomass (1.83 g/m^2) occurred in the Southern New England Slope area; the smallest (0.37 g/m^2) was in the Gulf of Maine.

Individual sipunculids averaged approximately 0.1 g in weight in all areas except Georges Slope, where their average weight was nearly forty times greater, 4 g per individual.

Frequency of occurrence of sipunculids was moderate to moderately low. They were present in 13 to 42% of the samples (Table 10). Highest frequency of occurrence was in the Nova Scotia area and lowest was on Georges Bank.

Bathymetric Distribution

Sipunculids were taken at depths ranging from 16 to 3,975 m. They were most common at moderate depths, 25 to 500 m, where they averaged about 6 to 8 individuals/m^2 (Table 11; Fig. 83). In both shallower and deeper zones they averaged nearly 1 or 2/m^2.

The relation between biomass of sipunculids and water depth was substantially different from that of numerical density. Biomass was much greater (averaging about 1 to 4 g/m^2) on the middle and lower portions of the continental slope (500 to 2,000 m) than it was on the continental shelf and continental rise (Table 13, Fig. 83). Also, sipunculids formed 10 to 26% of the total benthic biomass at these depths, compared with less than 1% for the shallower zones and 5% for the continental rise (Table 14).

The percentage of samples containing sipunculids was lowest (3 to 13%) at depths less than 50 m (Table 15). At depths greater

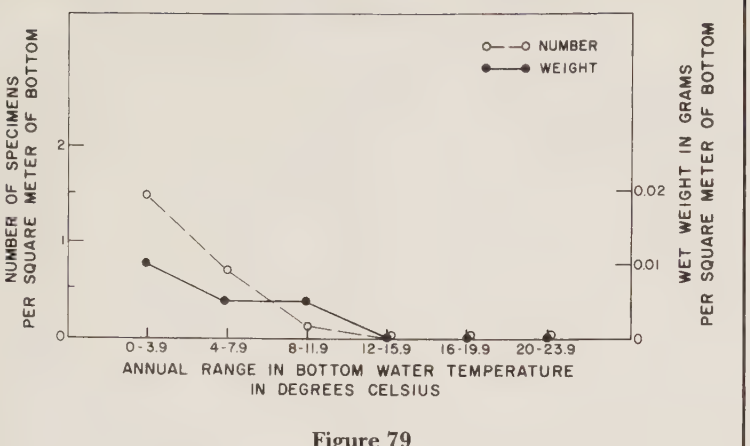


Figure 79
Density and biomass of Pogonophora in relation to the annual range of bottom water temperature.

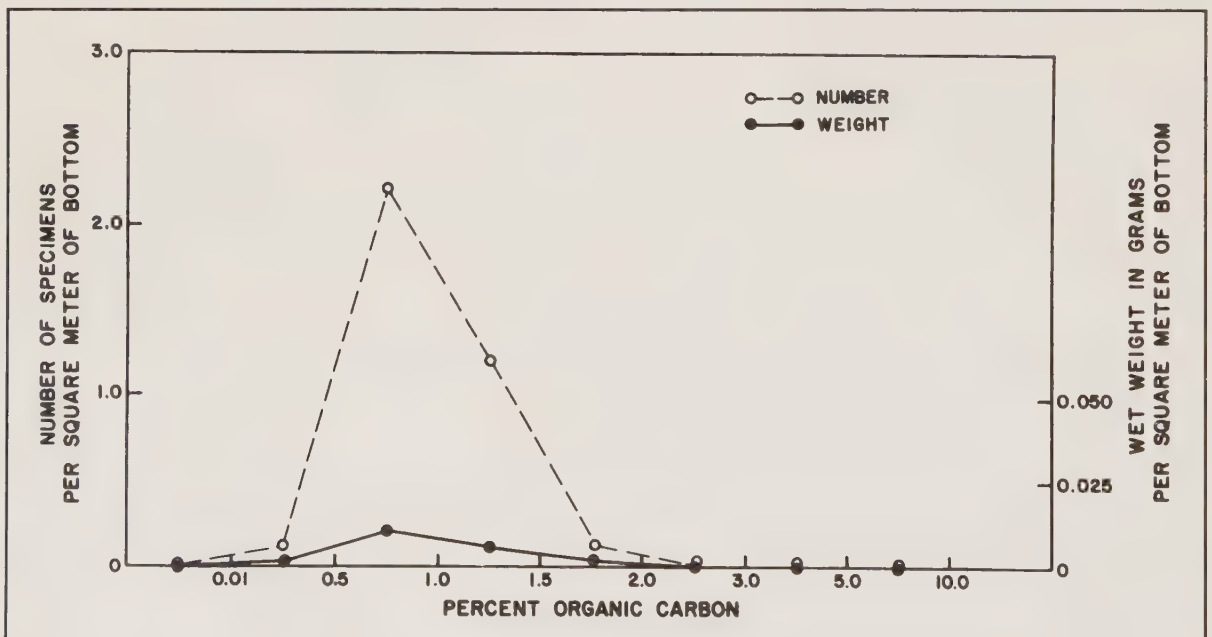
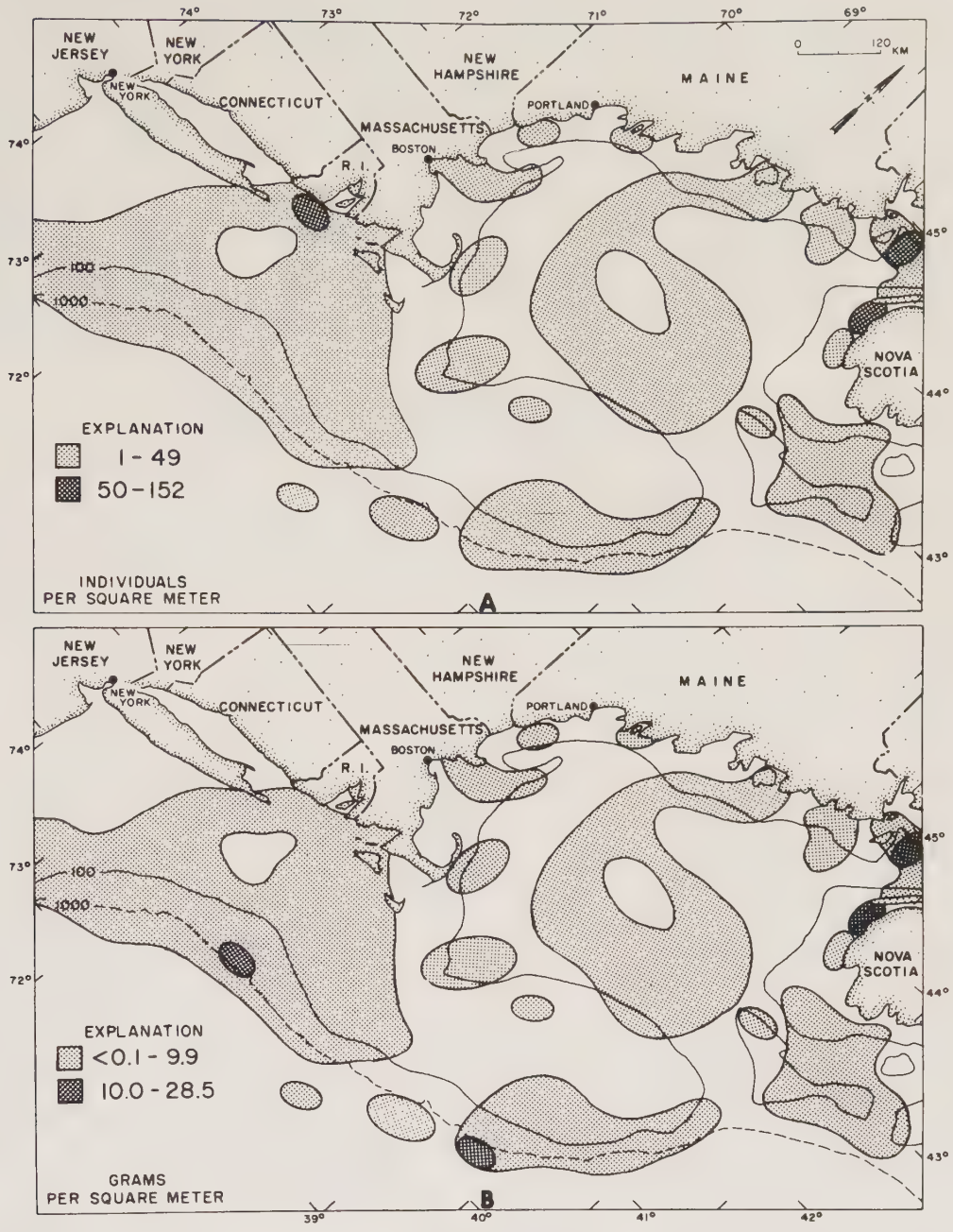


Figure 80
Density and biomass of Pogonophora in relation to sediment organic carbon.



SIPUNCULIDA

Figure 81

Geographic distribution of Sipunculida: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

than 50 m the percentage of occurrence ranged from 21 to 32%, with the highest rates occurring at depths <1,000 m and the lower rates at depths >1,000 m.

Relation to Sediments

Sipunculids inhabited all sediment types and occurred in about the same density in each type (Table 16; Fig. 84). The range in average density in the various types of bottom sediments was from 4.0 to 7.1/m^2. Sand contained the highest density.

Biomass of sipunculids in relation to various sediment types was considerably more varied than density of sipunculids (Table 18; Fig. 84). Biomass ranged from low values (0.16 to 0.29 g/m^2) in shell and till sub-

strates to high quantities (0.81 and 0.89 g/m^2) in sand and sand-silt.

Specimens from the shell substrates were the smallest in individual size.

Frequency of occurrence of sipunculids in the samples was moderately low and approximately equal among the different types of bottom sediments (Table 20). Range in percentage occurrence was 17 to 28, with highest values in sand and sand-silt; lowest values occurred in shell and silt-clay sediments.

Relation to Water Temperature

Sipunculid density, biomass, and frequency of occurrence generally tended to decrease as the range in temperature broadened (Fig. 85). None were found where the temperature range exceeded 20°C.

Density averaged about 5 to 9 individuals/m^2 where the temperature range was restricted and diminished to zero where the temperature range was most extensive (Table 21). The percentage of the total benthic fauna made up of sipunculids decreased at a rather uniform rate as the temperature range increased (Table 22).

Biomass of sipunculids was low or moderately low, and the changes in quantity in relation to temperature range followed precisely the same pattern as those in relation to density (Tables 23, 24). Biomass averaged about 0.7 to 1 g/m^2 in the narrow temperature range classes and decreased to zero where the temperature range was greater than 20°C. The percentage biomass composed of sipunculids also decreased as the temperature range expanded.

Frequency of sipunculids in the samples ranged from 0 to 29% (Table 25). They occurred most frequently, 25 to 29%, in samples where the temperature range was less than 12°C. Where the temperature range was broader than 12°C, the occurrence of sipunculids dropped substantially and they were absent in samples from areas where the temperature range was more than 20°C.

Relation to Sediment Organic Carbon

Sipunculids showed a decided preference for sediments with moderately low to low amounts of sediment organic carbon (Fig. 86). Both measures of abundance were greatest in the two classes between 0.01

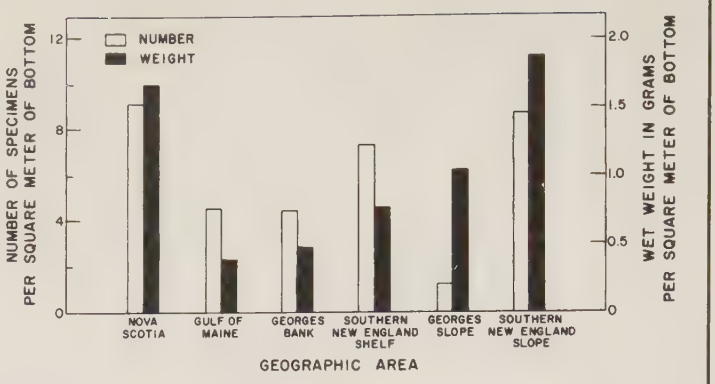


Figure 82

Density and biomass of Sipunculida in each of the six geographic areas.

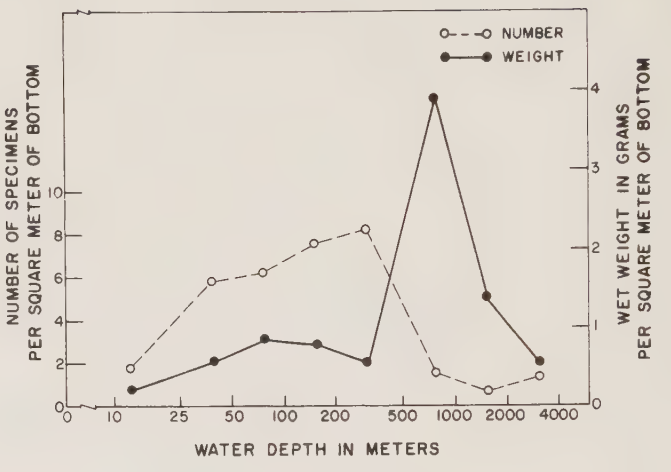


Figure 83

Density and biomass of Sipunculida in relation to water depth.

Figure 84

Density and biomass of Sipunculida in relation to bottom sediments.

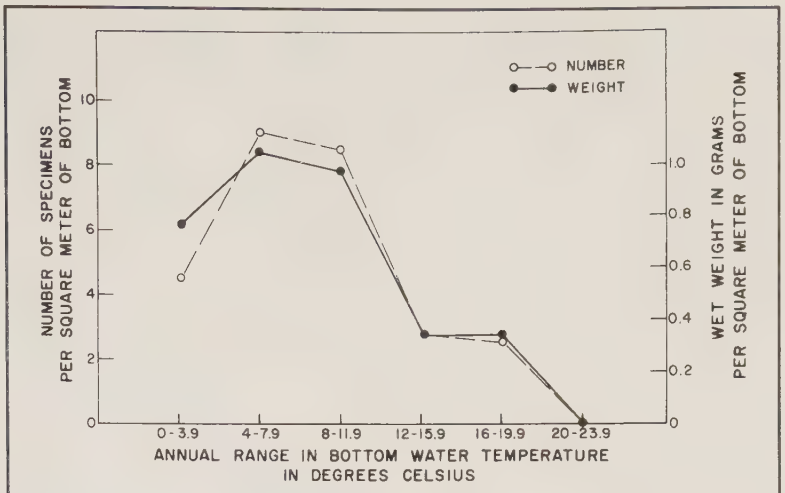


Figure 85
Density and biomass of Sipunculida in relation to the annual range of bottom water temperature.

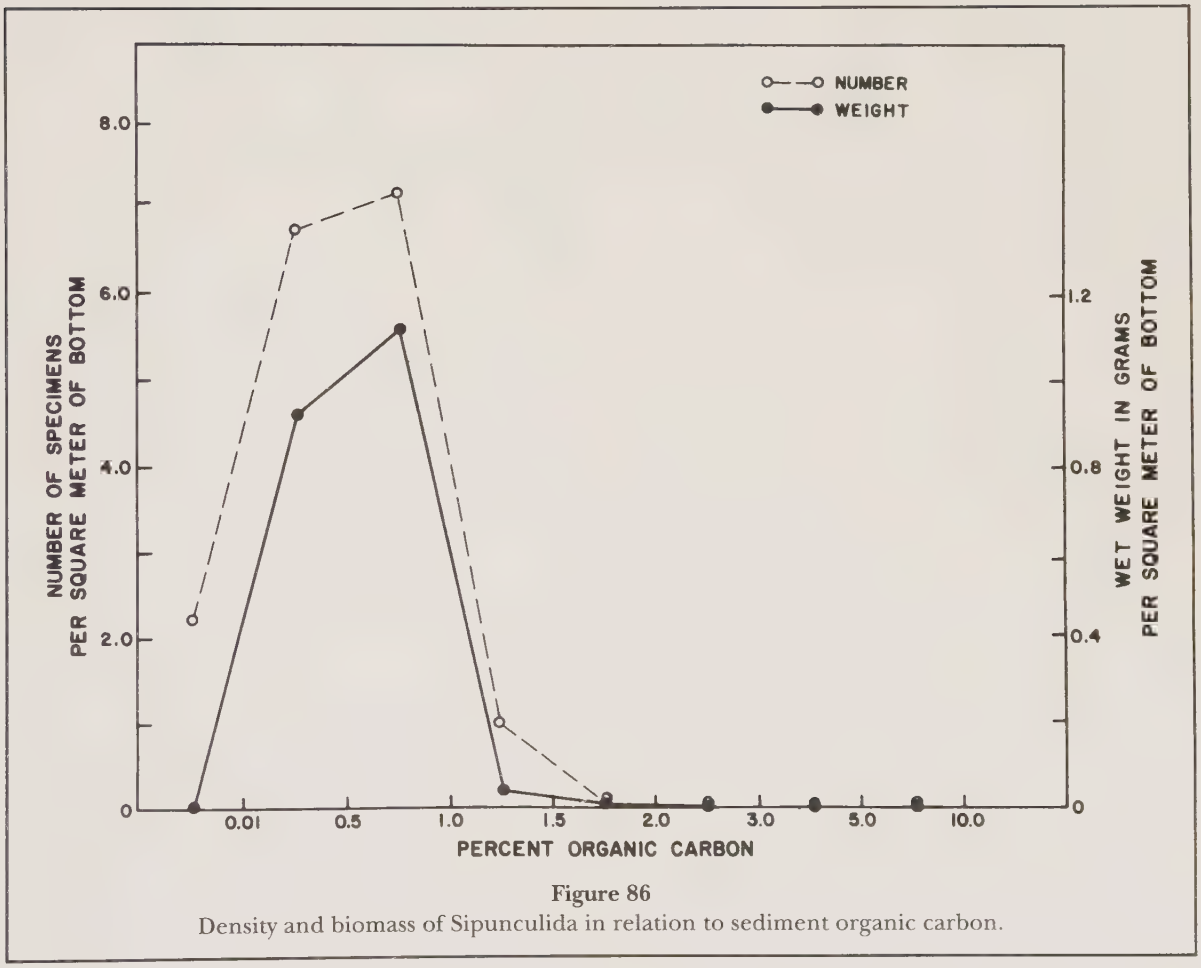


Figure 86
Density and biomass of Sipunculida in relation to sediment organic carbon.

and 0.99% organic carbon. Abundances were low where carbon was absent, but sipunculids were entirely absent in sediments whose carbon levels were 2% or greater.

Density of sipunculids ranged from 0.1 to slightly more than 7 individuals/m^2 (Table 26), and biomass ranged from <0.01 to a little more than 1.1 g/m^2 (Table 28).

Frequency of occurrence of sipunculids in the samples paralleled the trends established by density and biomass. Range of occurrence was from 2 to 31% (Table 30).

Echiura

Echiurid worms, like sipunculids and priapulids to which they are taxonomically allied and which they resemble somewhat in terms of size and habits, form a rather obscure and small group and are not very well known in this region. They are not especially abundant in the New England region, accounting for only 0.2% of total biomass and >0.1% of total density (Table 3).

Echiurids are round, unsegmented worms that typically burrow into sand and mud. Others are found among rocks and on coral reefs; one southern species uses the tests of sand dollars as a habitat.

Their size varies greatly, ranging from tiny 3-mm males to large females over 300 mm in length. Specimens in our samples were in the 2 to 8 cm size range.

They are reported to prefer shallow waters; however, the majority of our specimens were collected from deep water. Depth range of our samples was from 20 to 3,975 m, but only 5 of the samples were in water depths of less than 1,000 m.

Color of specimens ranges from drab grays and brown to green, red, and rose colored, and some were transparent.

Echiurids occurred in 17 samples (1.6% of total). Density averaged 0.1/m^2 and biomass 0.30 g/m^2 (Table 5).

Geographic Distribution

Echiurids were almost exclusively restricted in their geographic distribution to the lower continental shelf and upper continental slope and were found in rather small, discrete patches (Fig. 87). The only exceptions were two small areas inshore, one at the mouth of Long Island Sound and the other near Mt. Desert Island in the Gulf of Maine. Densities averaged between 1 and 9 individuals/m^2, whereas average biomass ranged from <0.1 to a high of 12.5 g/m^2.

Echiurids were absent from Nova Scotia and Georges Bank and were present in generally equitable densities in the other standard geographic areas. Highest average densities occurred in the two slope areas (Table 6; Fig. 88). Biomass was also highest in the slope area; significantly lower values were observed in the other areas in which they were found (Table 8; Fig. 88). Frequency of occurrence of echiurids in samples ranged from <1% to 15%. Lowest occurrence was in Gulf of Maine and highest on Georges Slope (Table 10).

Bathymetric Distribution

Echiurids were found at depths ranging from 20 to 3,975 m. Their numerical abundance was greatest, albeit low (0.5 to 0.6/m^2), in water depths greater than 1,000 m and even lower (0.02-0.3/m^2) at shelf and inshore depths (Table 11, Fig. 89).

The relation of biomass to water depth was similar to that of numerical density. Continental slope depths (1,000 to nearly 4,000 m) provided highest mean biomass of this small group ranging from 3.5 to 5 g/m^2. Significantly lower (0.22 to 0.01 g/m^2) biomasses occurred in inshore and midshelf depths, respectively (Table 13; Fig. 89).

Echiurids were found in 19 to 21% of the samples in the two depth range classes below 1,000 m, but in only <1% of the samples in the 100–199 m range and 2% in the 0–24 m range class (Table 15).

Relation to Sediments

Echiurids in our samples were rather restrictive in their choice of sediment, preferring to inhabit only the two finest-grained types. Both mean density (0.2 and 0.3/m^2) and biomass (0.79 and 0.69 g/m^2) were quite evenly apportioned between sand-silt and silt-clay, respectively (Tables 16, 18; Fig. 90). Three percent of the samples in sand-silt and 5% in silt-clay contained specimens (Table 20).

Relation to Water Temperature

Considering the deep water and fine sediment preferences of echiurids, it is not surprising to find that they also had restricted temperature preferences. They occupied only three temperature ranges; areas with the most stable annual range (0–3.9°C) contained the lowest density (0.1/m^2) but the highest biomass (0.9 g/m^2); areas with an annual range of 16–19.9°C had the highest density (0.4/m^2) and also contained the second highest biomass; and areas where the temperature range was between 4° and 7.9°C had moderate density and low biomass (Tables 21, 23; Fig. 91).

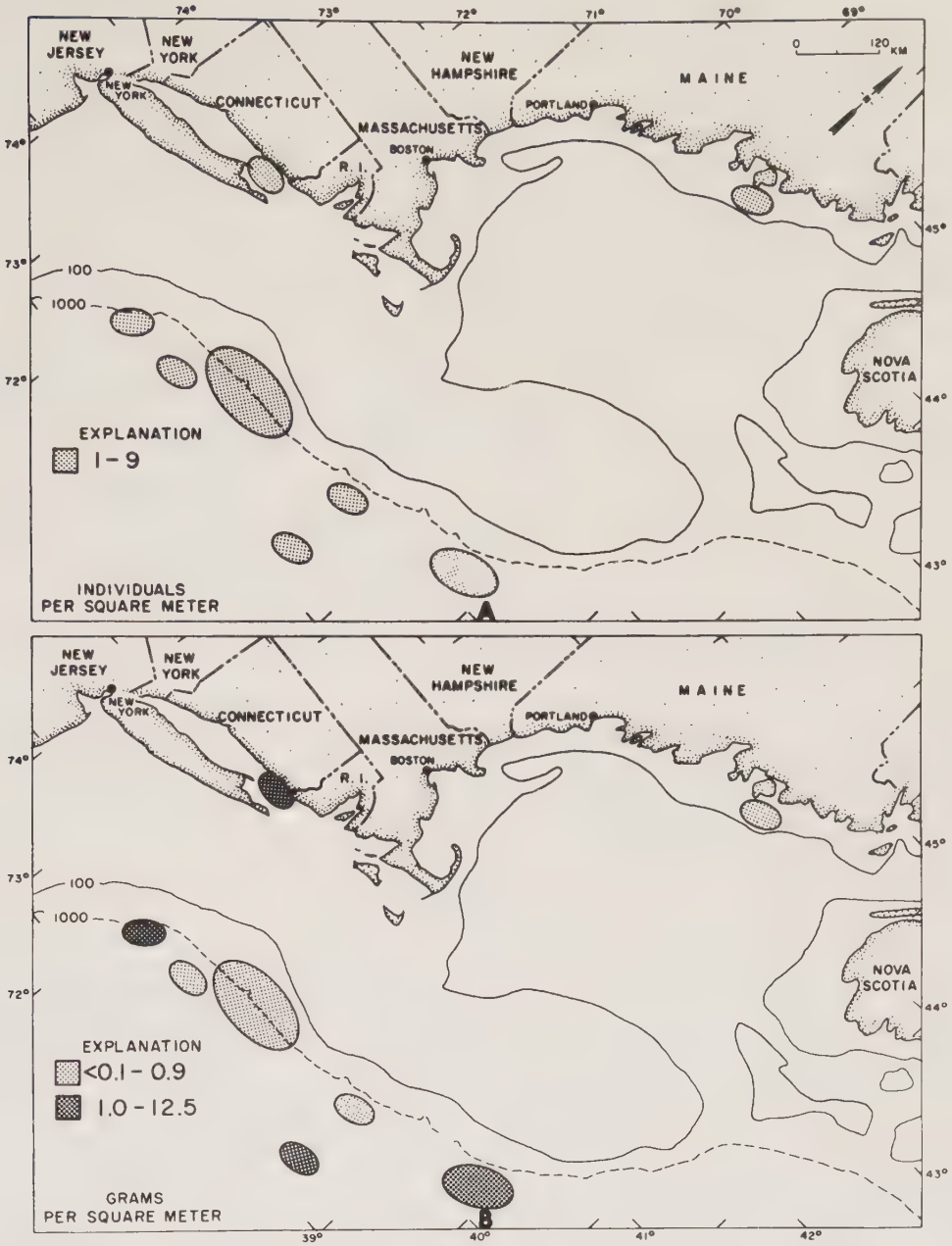
Frequency of occurrence ranged from 1 to 4% (Table 25), being highest in the narrowest temperature range.

Relation to Sediment Organic Carbon

Echiurids were also restrictive in relation to organic carbon content of sediments, occurring only where amounts ranged from 0.01 to 1.49% (Fig. 92). Density was greatest in carbon contents 0.50 to 0.99%, falling to lower levels in areas of both lesser and greater content (Table 26); conversely, biomass showed an increasing trend with organic carbon content (Table 28). Frequency of occurrence in samples reflected the trend for density (Table 30).

Priapulida

Among the invertebrate fauna of the New England region priapulid worms make up perhaps the rarest



ECHIURA

Figure 87

Geographic distribution of Echiura: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

and least known group; they are also uncommon in other areas of the world ocean as well—only eight species belonging to six genera have been reported (Barnes, 1974). Priapulids contributed <0.1% of the total number of specimens and biomass in the region (Table 3).

Priapulids are cucumber-shaped predacious worms that burrow into sand and mud and feed upon other soft-bodied, slow-moving invertebrates, especially polychaete worms. They are typically between 4 to 8 cm. in length. Our specimens were considerably smaller, in the 1 to 2 cm size range. Color of specimens ranges from whitish to flesh colored with some yellow on appendages; some of our specimens were somewhat reddish brown.

Only 4 (0.4% of total) of our samples yielded specimens (10 individuals weighing a total of 4.60 g) whose mean density was <0.1/m^2 and whose biomass was <0.01 g/m^2 (Table 5).

Priapulids in the New England region were found in the deep (1,420–2,035 m), cold (0–3.9°C), sand-silt and silt-clay bottoms of Georges and Southern New England Slope waters, where organic carbon levels range from 0.01 to 1.49%, in very low abundance (Figs. 93–98).

Mollusca

The phylum Mollusca contributes significantly to both measures of abundance (numerical density and biomass) in the New England region as it does in the Middle Atlantic Bight region (Wigley and Theroux, 1981). The molluscan fauna comprises five classes: Polyplacophora, Gastropoda, Bivalvia, Scaphopoda, and Cephalopoda. Each of these classes will be discussed separately below. For the sake of continuity in the phylogenetic ordering of figures, those figures dealing with phylum Mollusca (Figs. 99–104, inclusive) are included here, but a detailed discussion of the phylum as a whole will be presented in the section "Dominant Components of the Macrobenthos" below.

Polyplacophora—This class of mollusks is also called chitons, which are bilaterally symmetrical, have eight overlapping dorsal plates, and a broad, flat, ventral foot. They accounted for less than 1% of the biomass and number of animals of the total benthic invertebrate fauna (Table 3).

Specimens ranged in size from 4 mm to 2 cm and exhibited considerable variation in color. They were commonly chalky white or various shades of light gray; a small proportion were light brown. A few had a dark, nearly black coating over their plates that contrasted sharply with the underlying white or light gray.

Chitons were relatively common in the coastal areas, on relatively shallow offshore banks, on coarse bottom sediments, and where the water temperature range was moderately broad.

Polyplacophorans occurred in 84 samples (8% of total). Their density averaged 1.5/m^2, and biomass averaged 0.14 g/m^2 (Table 5).

Geographic Distribution

Polyplacophorans, although rather sparse, occurred in small to moderately large geographi-

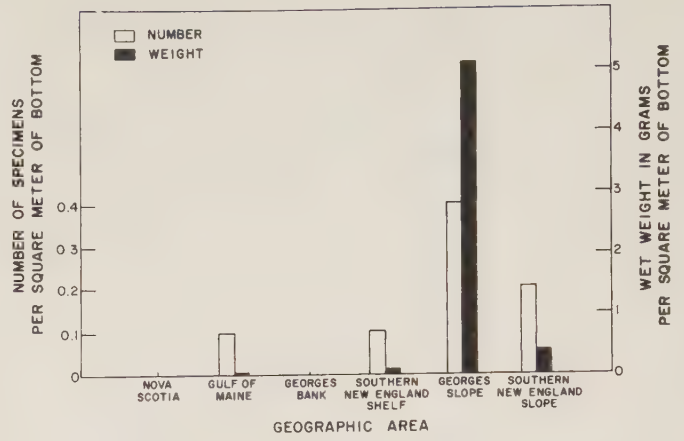


Figure 88
Density and biomass of Echiura in each of the six geographic areas.

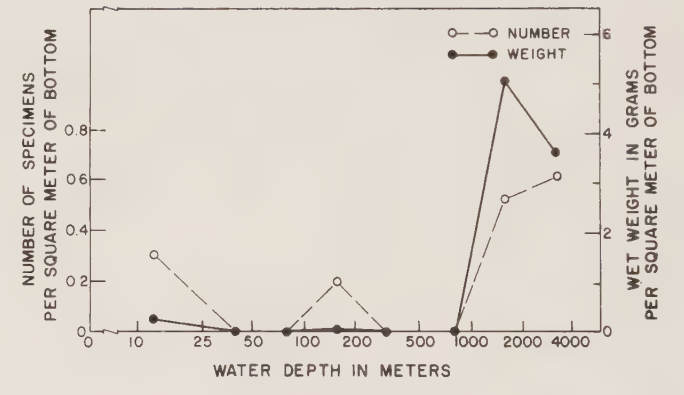


Figure 89
Density and biomass of Echiura in relation to water depth.

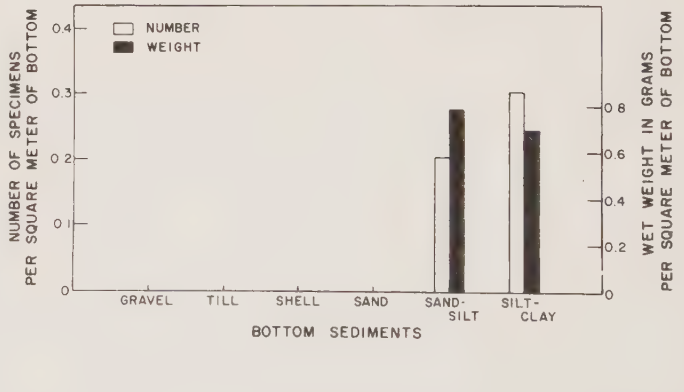


Figure 90
Density and biomass of Echiura in relation to bottom sediments.

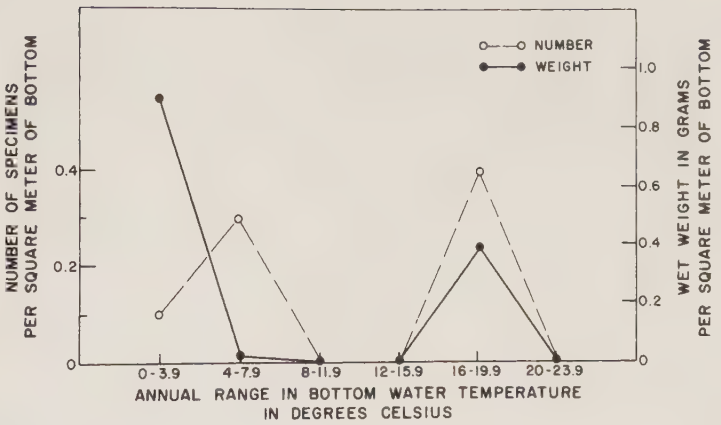


Figure 91
Density and biomass of Echiura in relation to the annual range of bottom water temperature.

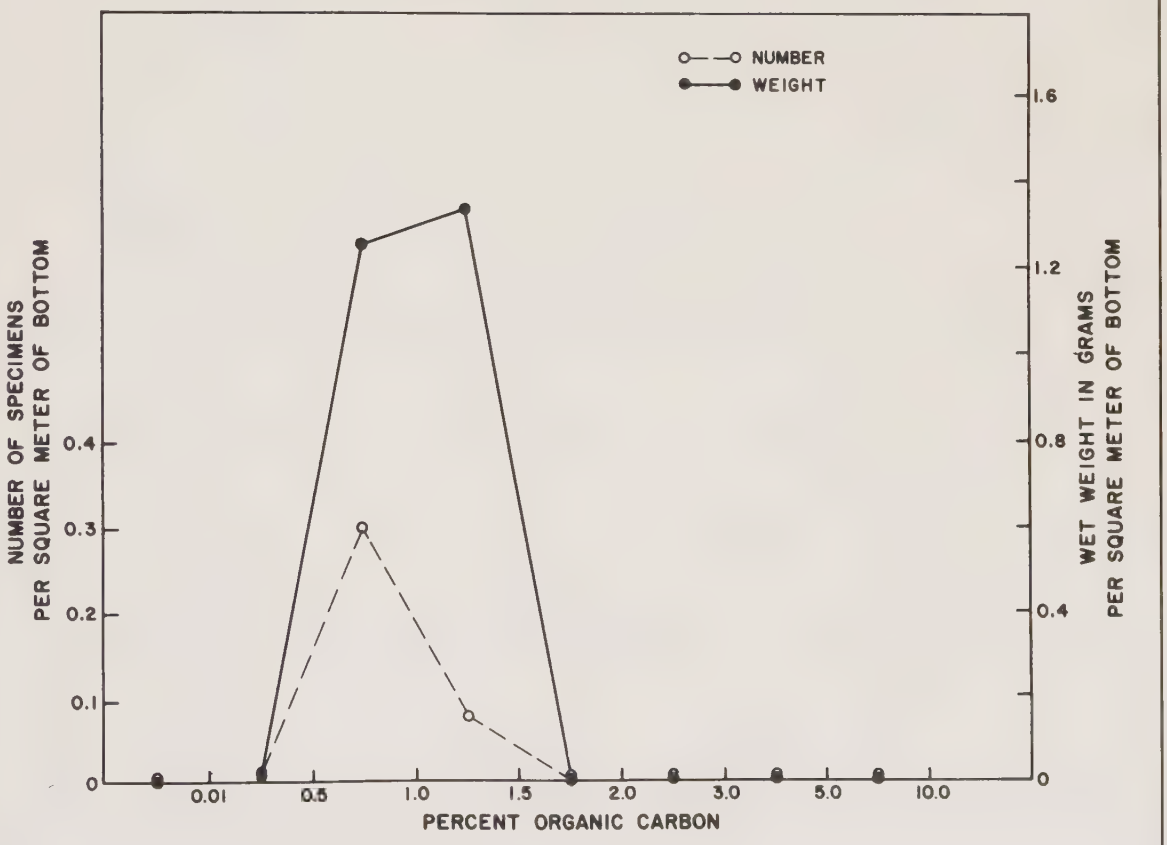
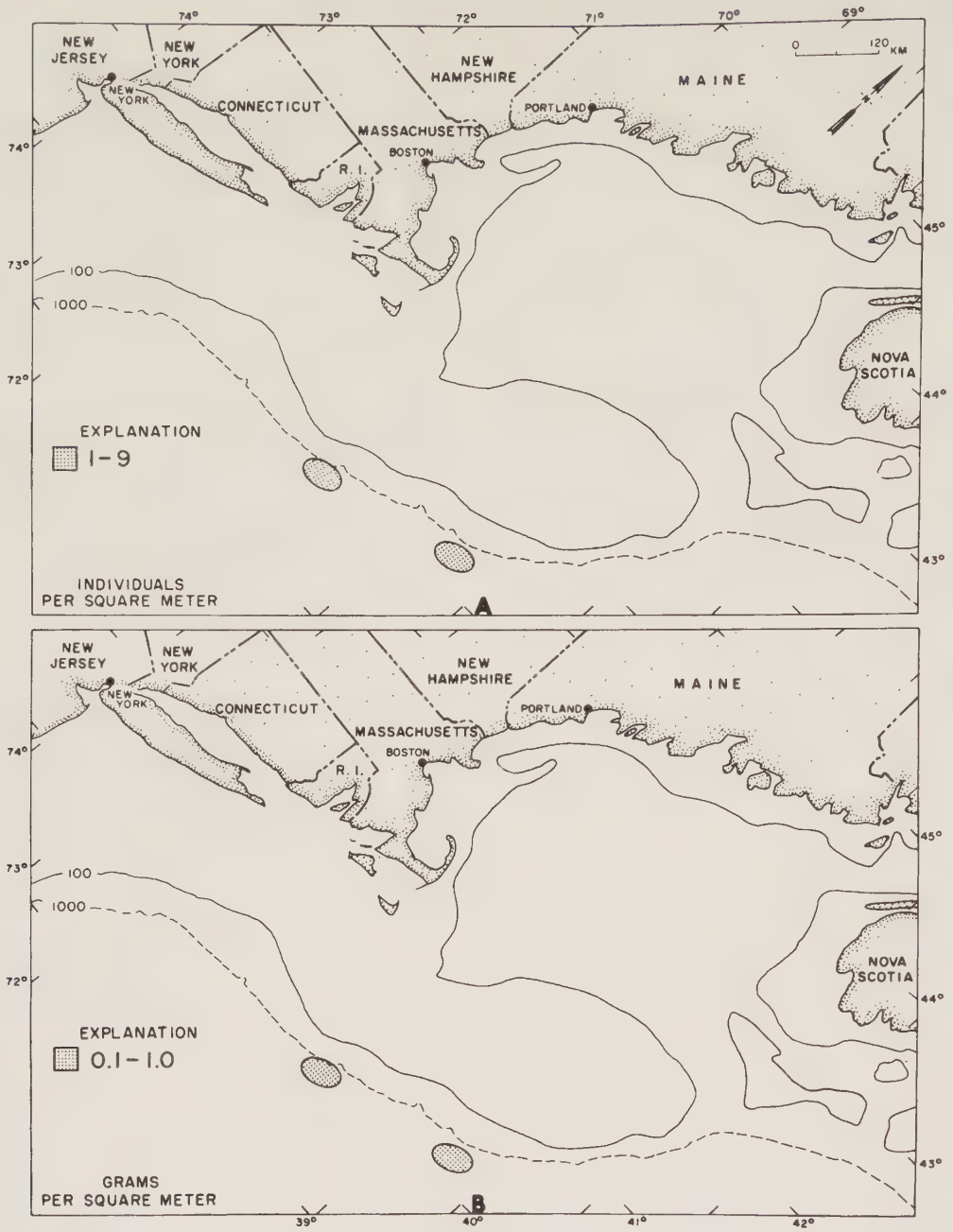


Figure 92
Density and biomass of Echiura in relation to sediment organic carbon.



PRIAPULIDA

Figure 93

Geographic distribution of Priapulida: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

cal areas throughout much of the study area (Fig. 105). They were most common in the Nova Scotia region, the periphery of the Gulf of Maine, in deep water south of Georges Bank, and on the outer shelf south of Cape Cod, Massachusetts. They were notably absent in the Georges Bank-Nantucket Shoals area and in deep water in the western Gulf of Maine. In all but a few locations their numerical density was less than $9/m^2$ and their weight averaged less than $1\ g/m^2$.

Three of the six standard geographic areas contained significant quantities of chitons: Nova Scotia, Gulf of Maine, and the Southern New England Shelf (Tables 6, 8; Fig. 106). The average number of specimens ranged from 0.9 to $3.6/m^2$. Average biomass was small, $0.24\ g/m^2$

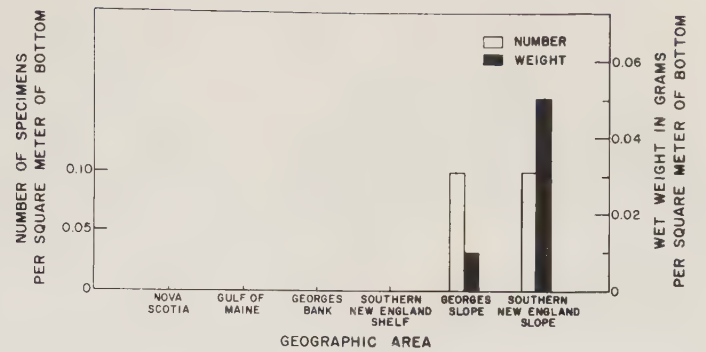


Figure 94
Density and biomass of Priapulida in each of the six geographic areas.

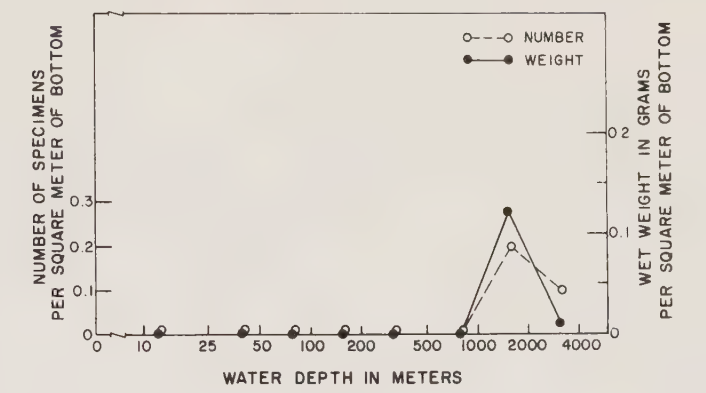


Figure 95
Density and biomass of Priapulida in relation to water depth.

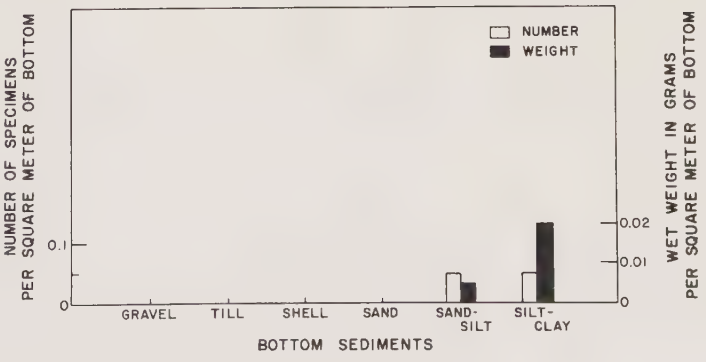


Figure 96
Density and biomass of Priapulida in relation to bottom sediments.

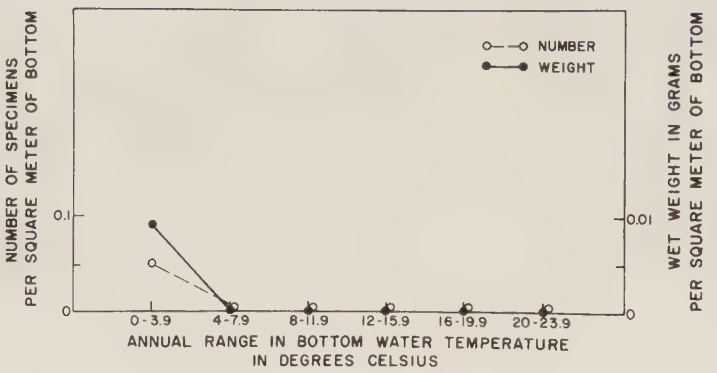


Figure 97
Density and biomass of Priapulida in relation to the annual range of bottom water temperature.

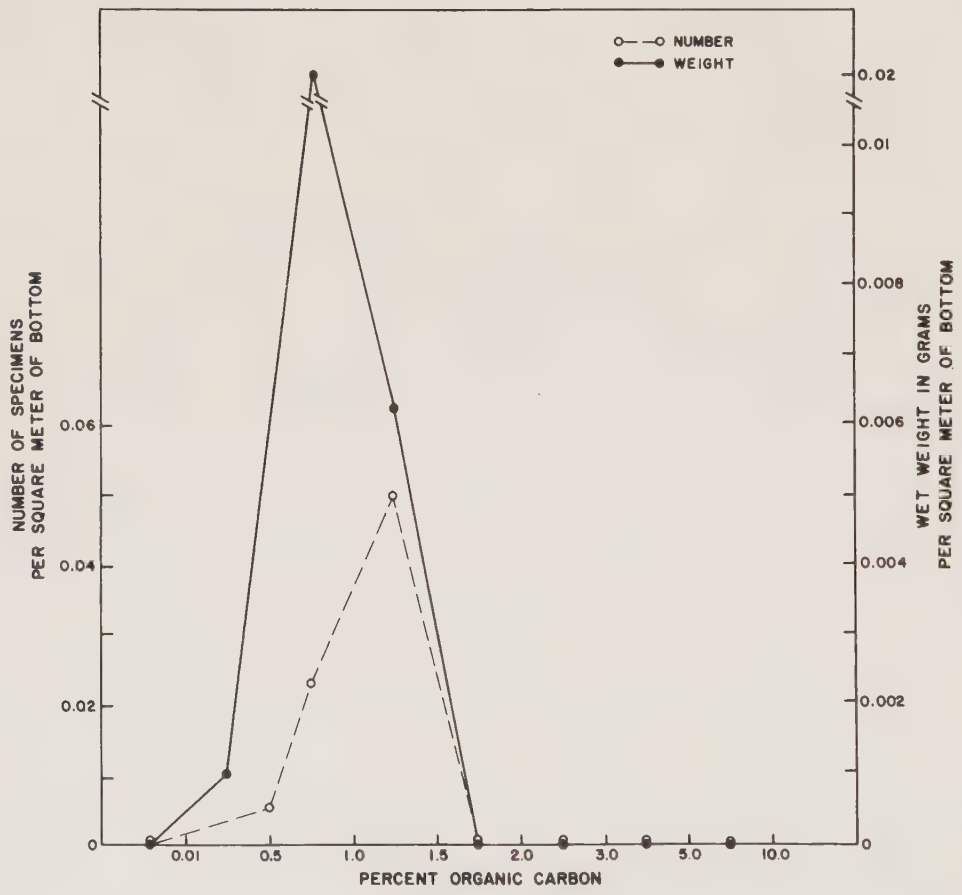
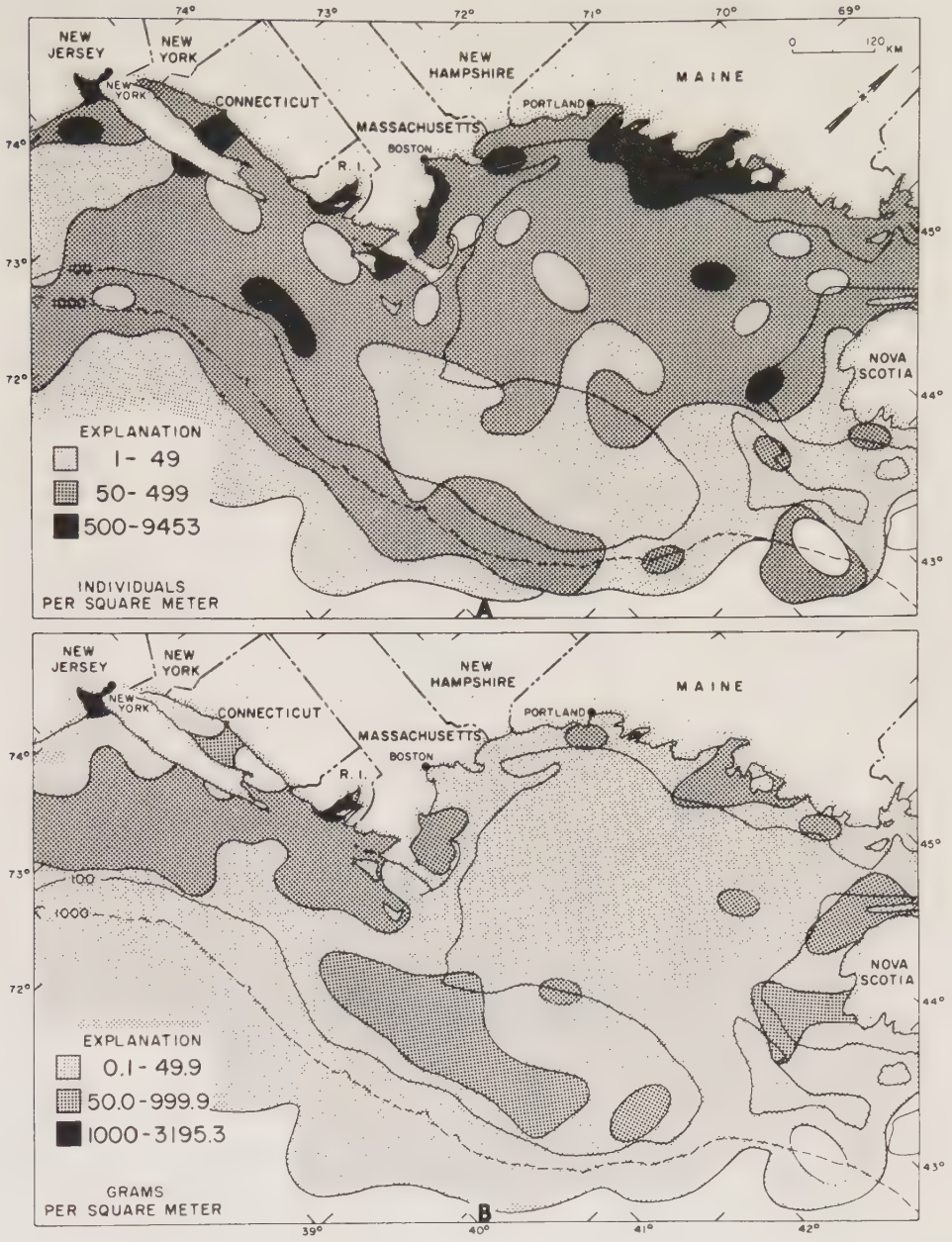


Figure 98
Density and biomass of Priapulida in relation to sediment organic carbon.



MOLLUSCA

Figure 99

Geographic distribution of Mollusca: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

or less. On Georges Bank, Georges Slope, and the Southern New England Slope their density averaged 0.1 to 0.6/m^2, and their weight averaged 0.01 g/m^2 or less.

Frequency of occurrence was relatively high (1 to 24%) considering the small quantities that were present (Table 10). This high frequency of occurrence is simply a reflection of their small size and wide dispersion. Individuals were especially small in the Georges Slope area and relatively larger in the Southern New England Shelf area.

Bathymetric Distribution

Polyplacophorans were present at depths from 16 to 2,840 m. They were more abundant in shallow and moderate depths than in very deep water (Table 11; Fig. 107). Average density in depth classes less than 500

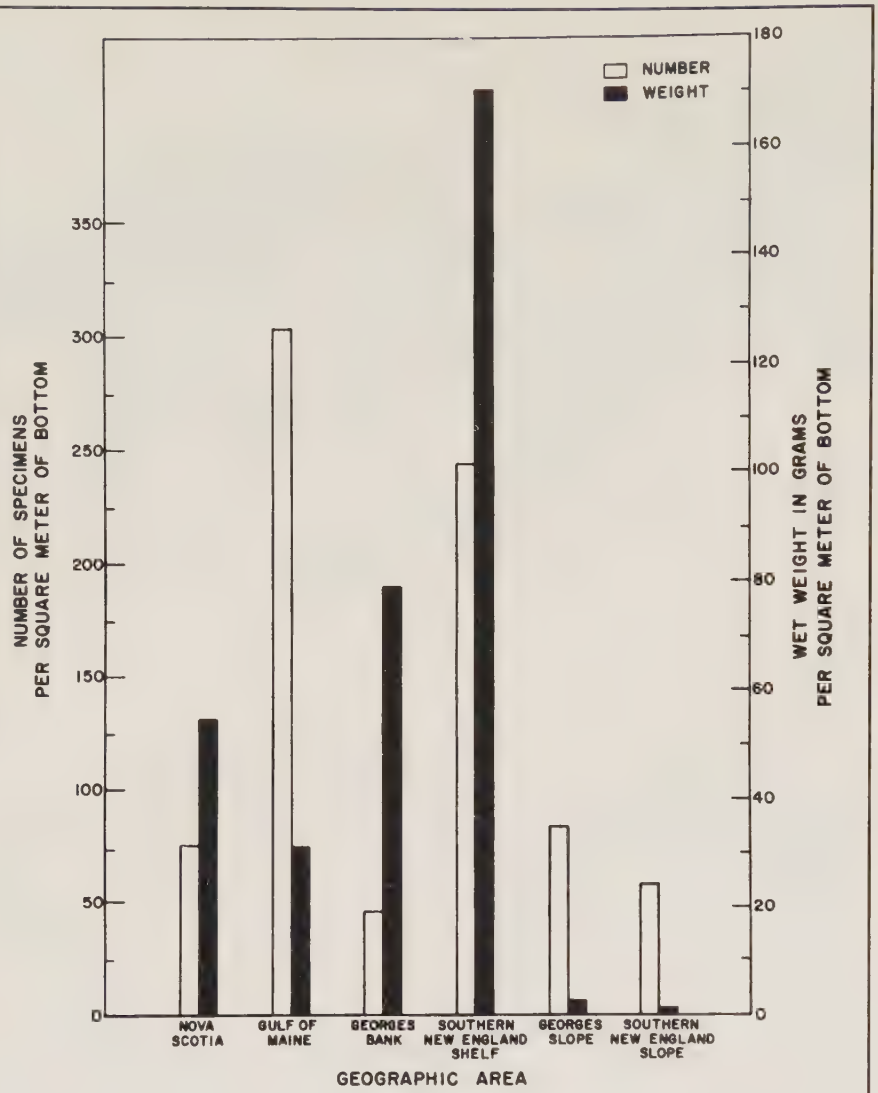


Figure 100
Density and biomass of Mollusca in each of the six geographic areas.

m ranged from 0.4 to 4.0/m^2. Below 500 m the average density in the various depth classes was 0.2 to 0.5/m^2.

Average biomass of chitons was greater (0.3 to 0.8 g/m^2) at depths less than 500 m than in the deeper water where their biomass averaged 0.01 g/m^2 or less (Table 13; Fig. 107).

Frequency of occurrence was low (1 to 18%) and no clear relations with depth were evident. The trend indicated a slightly higher rate of occurrence in moderate (50 to 200 m) and deep (>200 m) water (Table 15).

These results indicate that polyplacophorans are less abundant but more uniformly distributed in deep water (>500 m) than on the continental shelf and upper portion of the continental slope.

Relation to Sediments

Polyplacophorans occurred in all sediments except shell (Table 16; Fig. 108). Highest density (3.8/m^2) was encountered in sand-silt sediment. Till, gravel, and silt-clay ranked second to fourth, respectively, and only very small quantities (0.3/m^2) were found in sand sediments.

The relationship of average biomass to various types of bottom sediments was quite different from that of density (Table 18; Fig. 108). Gravel and till yielded the largest biomasses (0.7 and 0.3 g/m^2, respectively), whereas in all other sediments it averaged <0.07 g/m^2.

Frequency of occurrence was highest (11 to 27% of the samples) in those sediments where chitons were

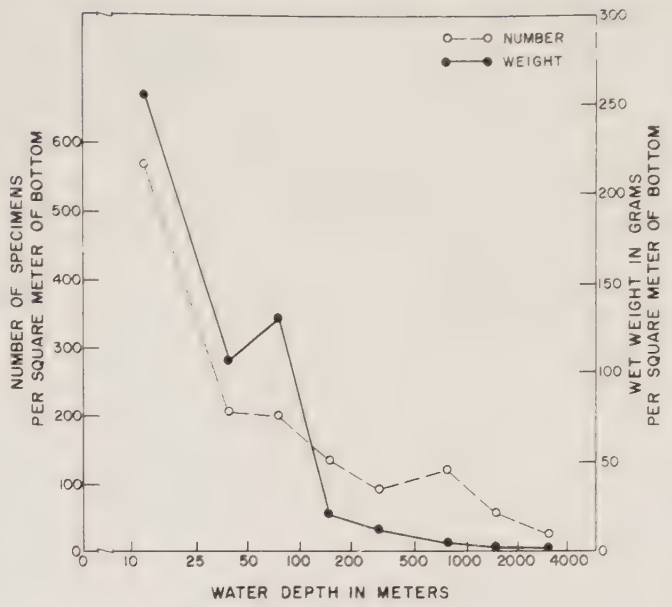


Figure 101
Density and biomass of Mollusca in relation to water depth.

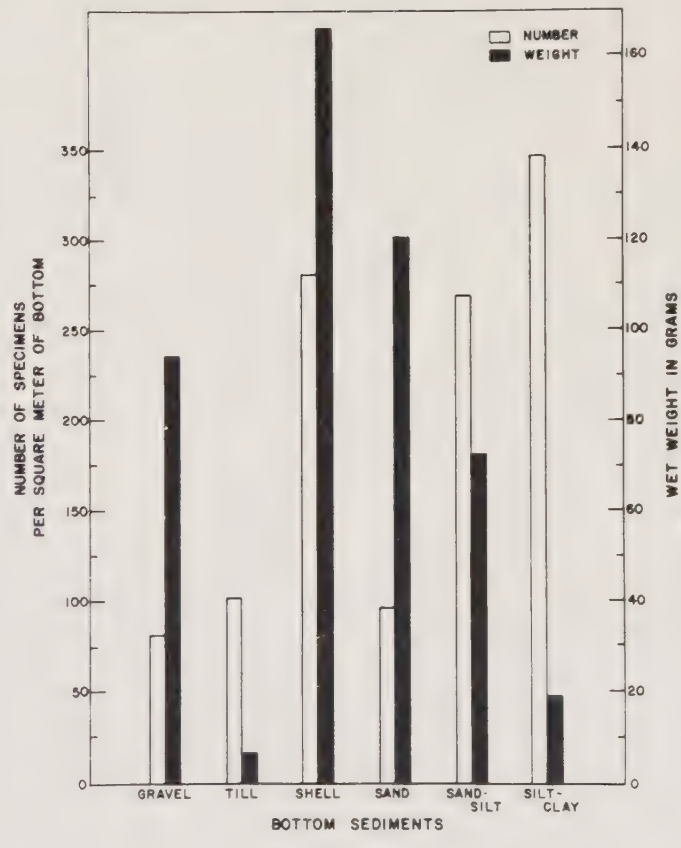


Figure 102
Density and biomass of Mollusca in relation to bottom sediments.

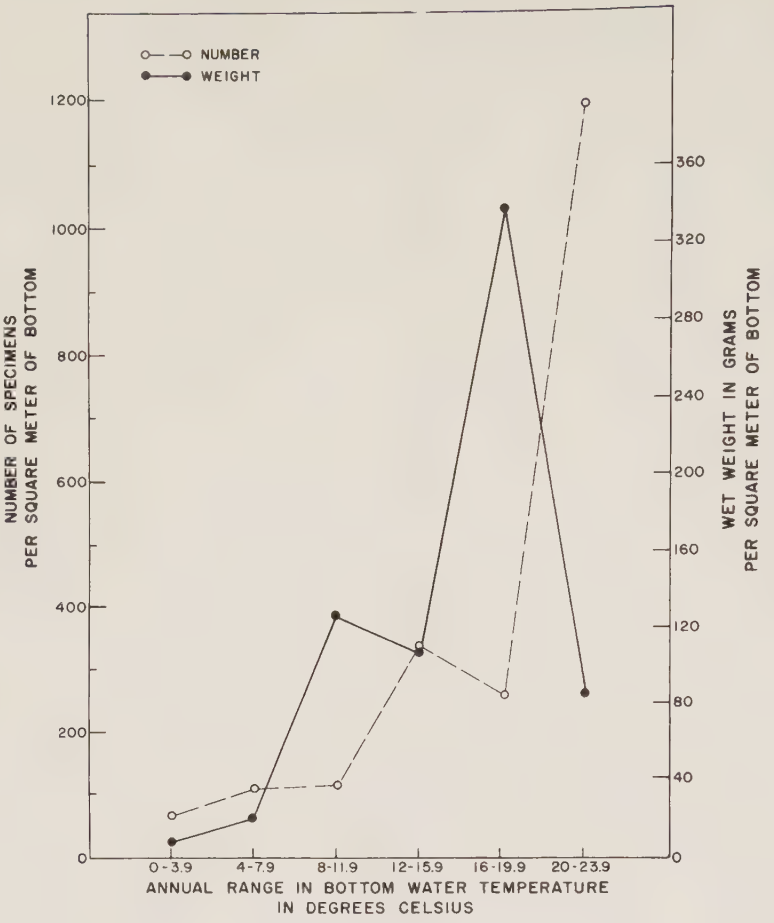


Figure 103
Density and biomass of Mollusca in relation to the annual range of bottom water temperature.

most numerous, namely till, gravel, and sand-silt (Table 20). Their occurrence rate was low (3 to 9% of the samples) in sand and silt-clay.

Relation to Water Temperature

Polyplacophorans were found to inhabit a rather broad span of annual ranges in water temperature, from 0–3.9° to 16–19.9°C, inclusive (Table 21, Fig. 109). They were numerous; average density was 7.3/m^2, where the water temperature range was greatest. Lower densities (0.8 to 1.4/m^2) were found in the middle and low temperature range groupings.

Biomass values in relation to water temperature range rather closely paralleled the trends described above for density (Table 23; Fig. 109). At the greater temperature range, 16° to 19.9°C, the biomass averaged 1.3 g/m^2, whereas in the middle and lower range groupings, the biomass averaged 0.12 g/m^2 or less.

Frequency of occurrence was low in all temperature ranges but was relatively higher (10%) where the fluctuation in temperature was less than 8°C (Table 25). Occurrence rate was relatively moderate (5 to 7%) where the temperature range was moderate. No chitons were taken where the temperature range was greater than 20°C.

Relation to Sediment Organic Carbon

Polyplacophorans were rather restricted in their distribution in relation to the quantity of organic carbon in the sediments, occurring only where the carbon content ranged from 0.01 to 1.99% (Table 26; Fig. 110). Average density was highest (2.5 /m^2) in the lowest carbon content class (0.01–0.49%), lower still (1/m^2) in the 1 to 1.5% content class; and significantly lower in the other two classes they occupied.

Average biomass decreased markedly from its highest point (0.25 g/m^2) in the lowest content class (0.01–

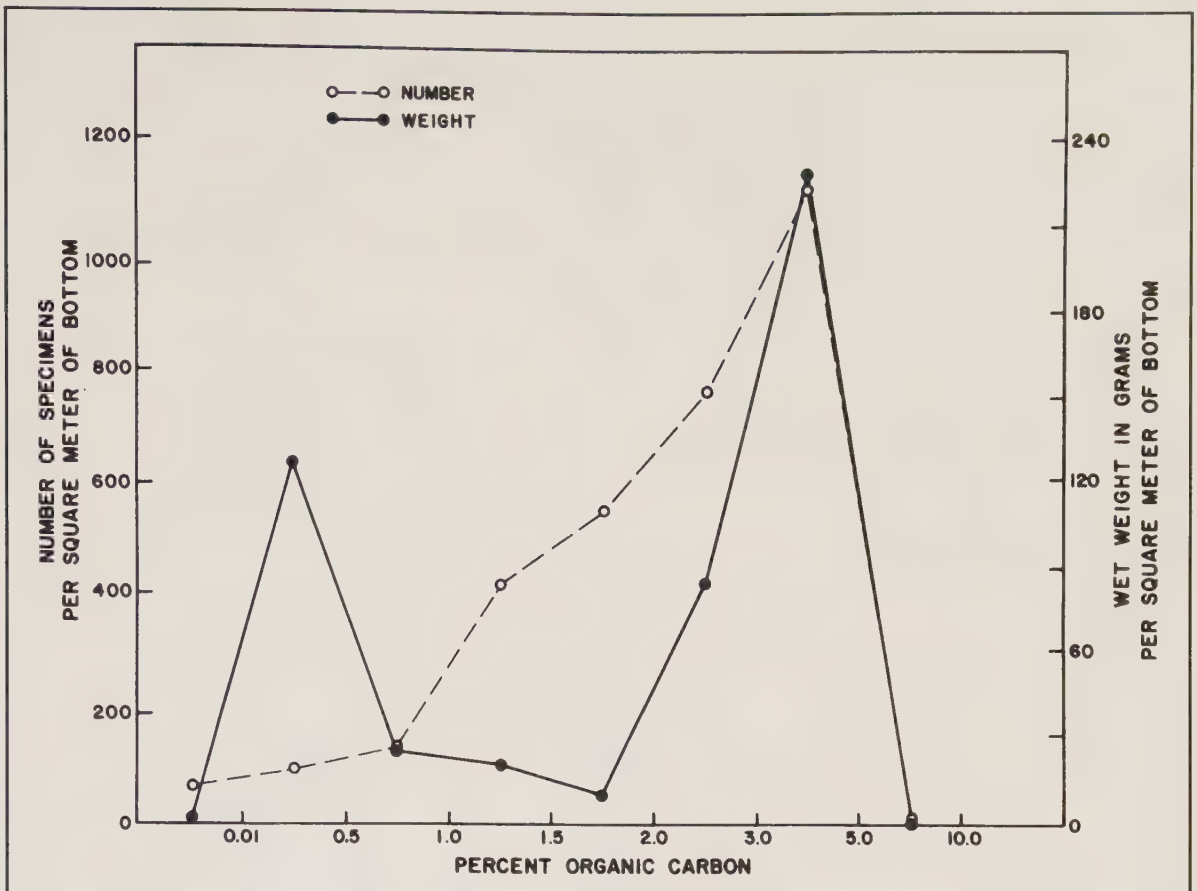


Figure 104
Density and biomass of Mollusca in relation to sediment organic carbon.

0.49%) to very small (<0.01 g/m^2) as carbon content increased to just under 2% (Table 28; Fig. 110).

Frequency of occurrence in samples exhibited a trend similar to that of biomass. Incidence was relatively low (ranging from 2 to 12%) and diminished with increasing carbon content (Table 30).

Gastropoda—Gastropods formed a moderately common component of the New England benthos. They were distributed throughout most of the study area, but because of their generally small size they accounted for only a small proportion (1.2%) of the total benthic biomass (Table 3).

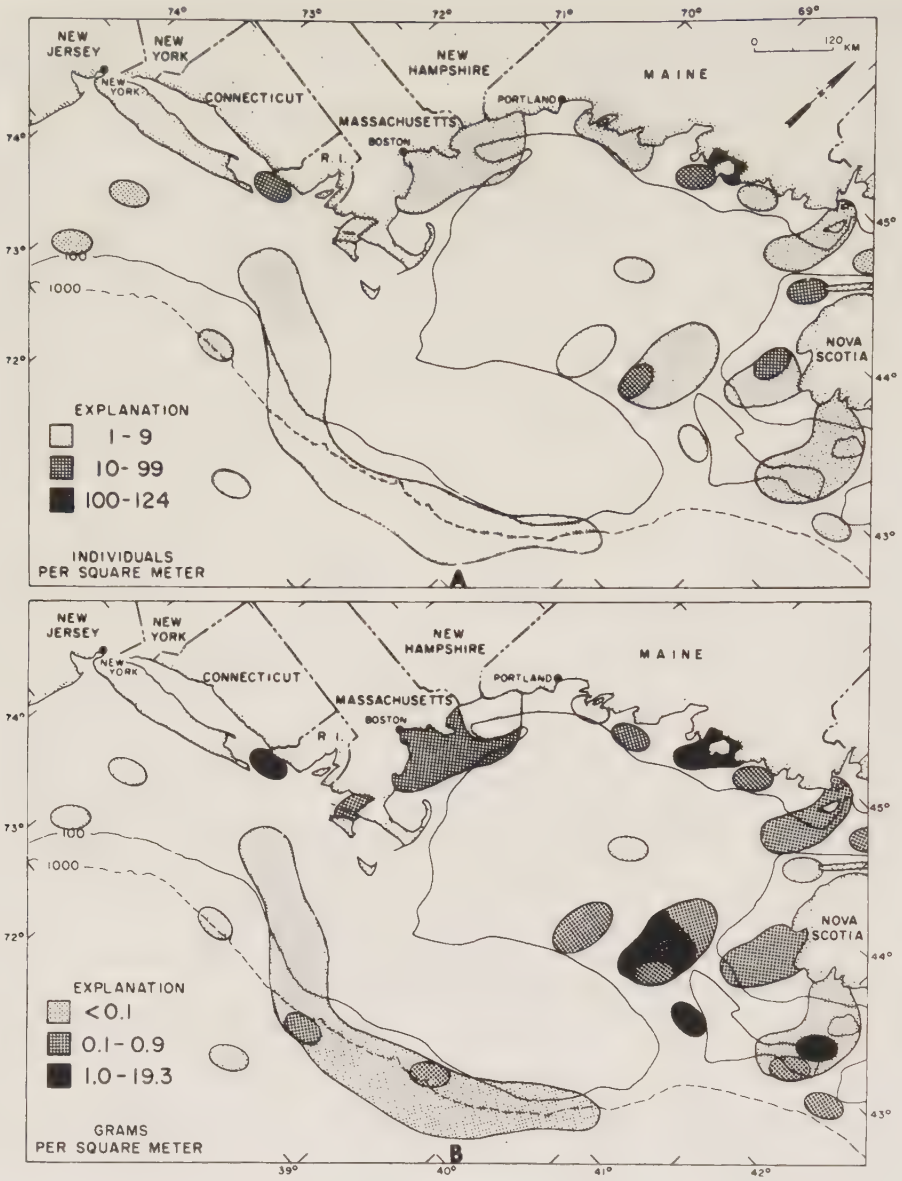
These mollusks varied enormously in size, from the tiny *Retusa* and *Alvania* (approximately 2 mm in length) to large specimens of *Neptunea, Colus, Busycon,* and *Buccinum* (ranging up to 13 cm or more). The majority of specimens were between 2 and 30 mm.

Shelled gastropods were predominant in our collections, although some shell-less groups (Nudibranchia and Aplysiacea) were represented. Nudibranchs were abundant in a few localized shallow water habitats but were generally uncommon to rare in the offshore regions.

Specimens in our samples were usually drab colored, with various shades or combinations of white, gray, and brown predominating. The shell-less groups contained some of the more brightly colored forms. In these groups light yellow, pink, orange, and rusty-red hues were common on the dorsal body surface and in the cerata and tentacles.

Gastropods of different taxonomic groups obtain their nourishment by a variety of methods. Feeding types known to be represented in our collections were herbivores, predacious and nonpredaceous carnivores, and parasites. Carnivores and scavengers that feed heavily on bivalve mollusks were the largest and most common forms encountered. Parasitic species were rare.

Gastropods occurred in 470 samples (44%). Their density averaged 8/m^2; biomass averaged 2.2 g/m^2 (Table 5).



POLYPLACOPHORA

Figure 105

Geographic distribution of Polyplacophora: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

Geographic Distribution

Gastropods were distributed over nearly the entire region (Fig. 111). Moderately low densities (1 to 49 individuals/m^2) were widespread over a large part of the study area. Medium and high densities generally occurred in limited areas inshore and nearshore.

In most areas where gastropods were found, their average biomass was less than 1 g/m^2. Moderately high biomasses (1 to 25 g/m^2) occurred over rather large areas both inshore and offshore, whereas large biomasses (25 to 133 g/m^2) occurred in only four localities.

Gastropods were present in all six of the standard geographic areas (Tables 6, 8; Fig. 112). Quantities, in terms of both number of individuals and biomass, were highest in the four continental shelf areas and lowest in the Georges Slope and Southern New England Slope areas. Average density in the shelf areas ranged from 11 to 29 individuals/m^2 and average biomass from 0.9 to 4.3 g/m^2. In the slope areas the average density was 7 to 8 individuals/m^2 and average biomass was less than 0.3 g/m^2. Gastropods made up a slightly higher proportion of the total faunal density in the slope areas than they did in the continental shelf areas.

Frequency of occurrence of gastropods was moderately high in all geographic areas. They were present in 35 to 58% of the samples (Table 10). The high frequency of occurrence in the Georges Slope and Southern New England Slope areas, in comparison to the low density and small average biomass in these areas, is indicative of small-size specimens and of rather widespread and uniform distribution.

Bathymetric Distribution

Gastropods occurred at water depths ranging from 3 to 3,310 m. They were far more abundant ($64/m^2$) in shallow water (0 to 24 m) than at other depths. Their average density (Table 11; Fig. 113) generally diminished with increasing water depth, except for a slight reversal of this trend on the upper and middle sections of the continental slope. Density was roughly uniform (11 to 24 individuals/m^2) between 25 and 1,000 m. In the two deepwater classes the densities were considerably lower (4 and $1/m^2$).

Average biomass also was largest in shallow water and smallest in deep water (Table 13; Fig. 113). The average biomass in all depth classes on the continental shelf was moderate (1.1 to 4.8 g/m^2), whereas at all depths greater than 200 m the average biomass was small (0.15 to 0.29 g/m^2).

Frequency of occurrence of gastropods was moderately high (37 to 52%) on the continental shelf and upper slope (Table 15). At mid- and lower-slope depths occurrence was high (74 to 77%). On the continental rise their rate of occurrence diminished to only 30%.

Relation to Sediments

Although there was no consistent trend in density of gastropods in relation to sediment particle size, there were several correlative points of interest (Table 16; Fig. 114). Gastropods occurred in particularly high densities in shelly sediments, where their average concentration was 83 individuals/m^2. Presumably these gastropods were predators on the bivalves whose shells formed the substrate. Densities were also high ($40/m^2$) on gravel bottoms. In all other sediment types they occurred in only moderate densities (9 to 22 individuals/m^2). The unexpectedly low density of $9/m^2$ in till substrates indicates that till is more closely allied to silt-clay as a gastropod habitat than it is to gravel. Just the reverse is true for other molluscan groups.

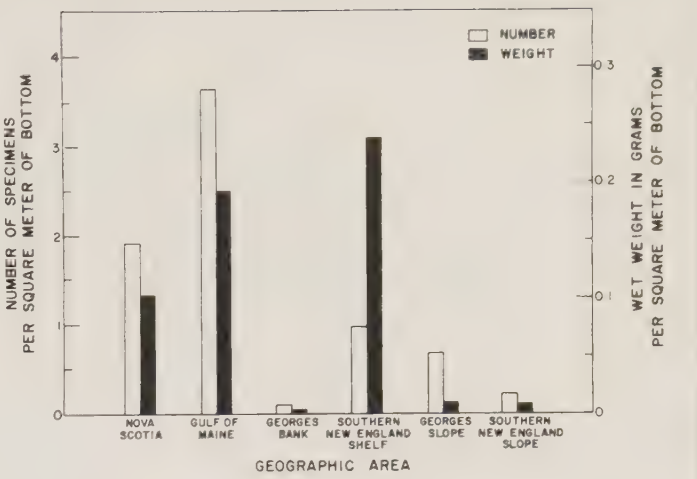


Figure 106

Density and biomass of Polyplacophora in each of the six geographic areas.

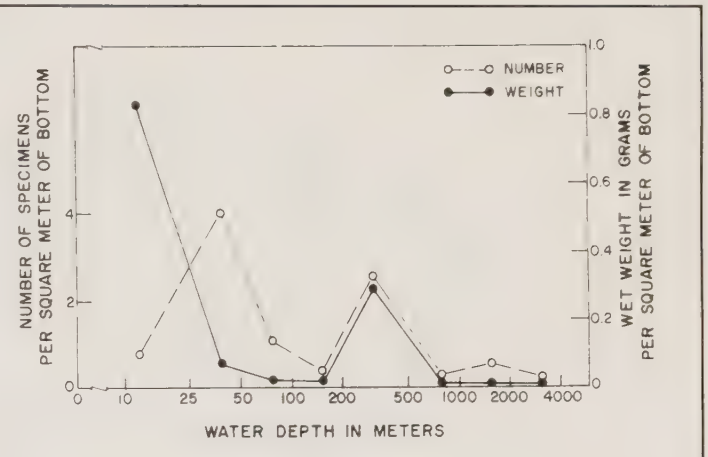


Figure 107

Density and biomass of Polyplacophora in relation to water depth.

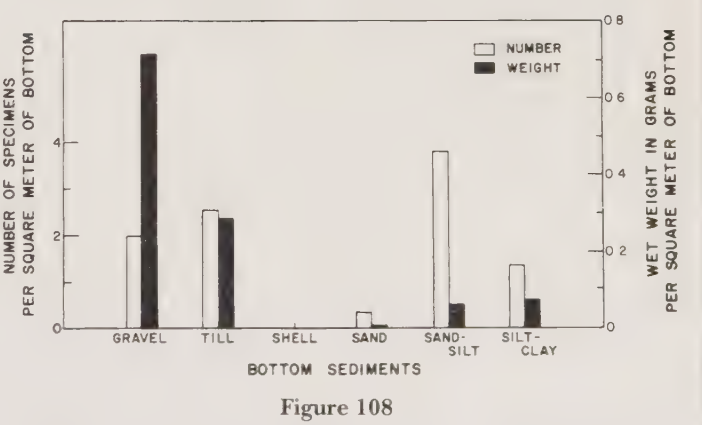


Figure 108

Density and biomass of Polyplacophora in relation to bottom sediments.

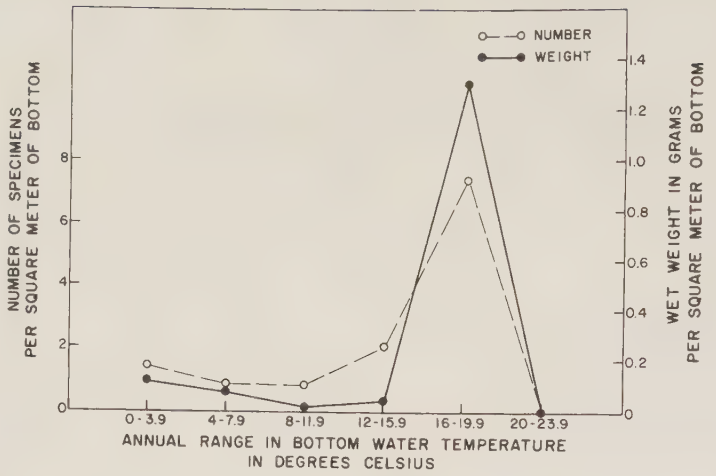


Figure 109
Density and biomass of Polyplacophora in relation to the annual range of bottom water temperature.

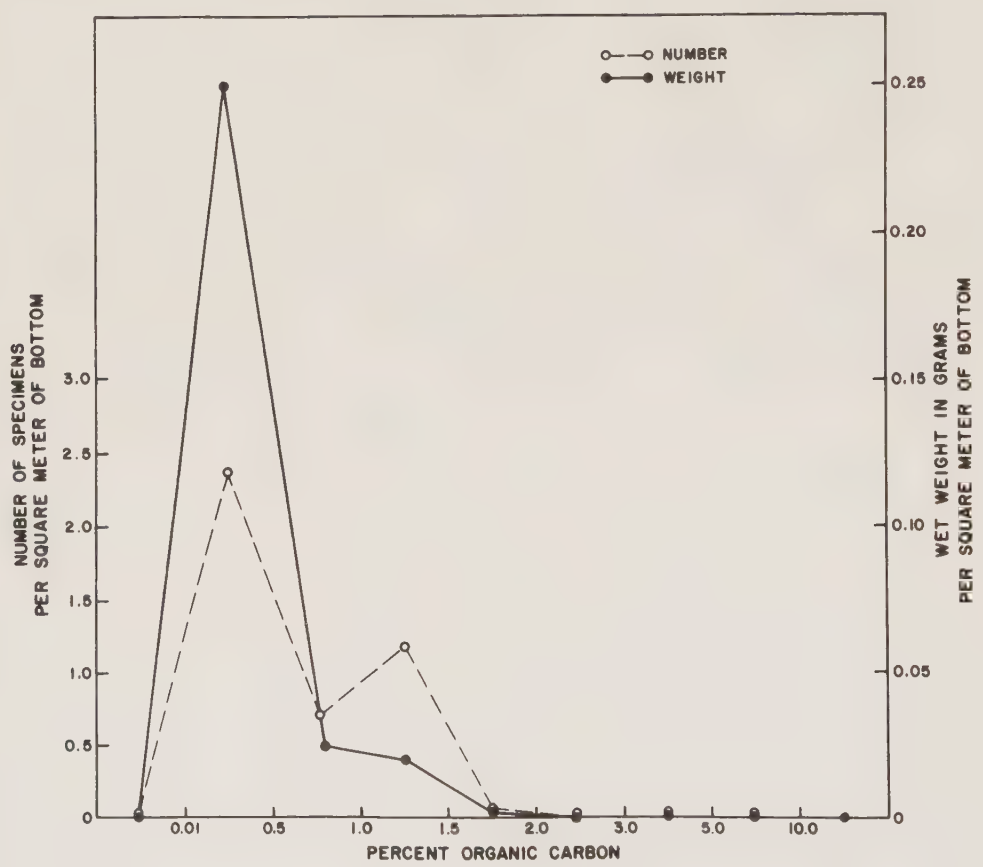
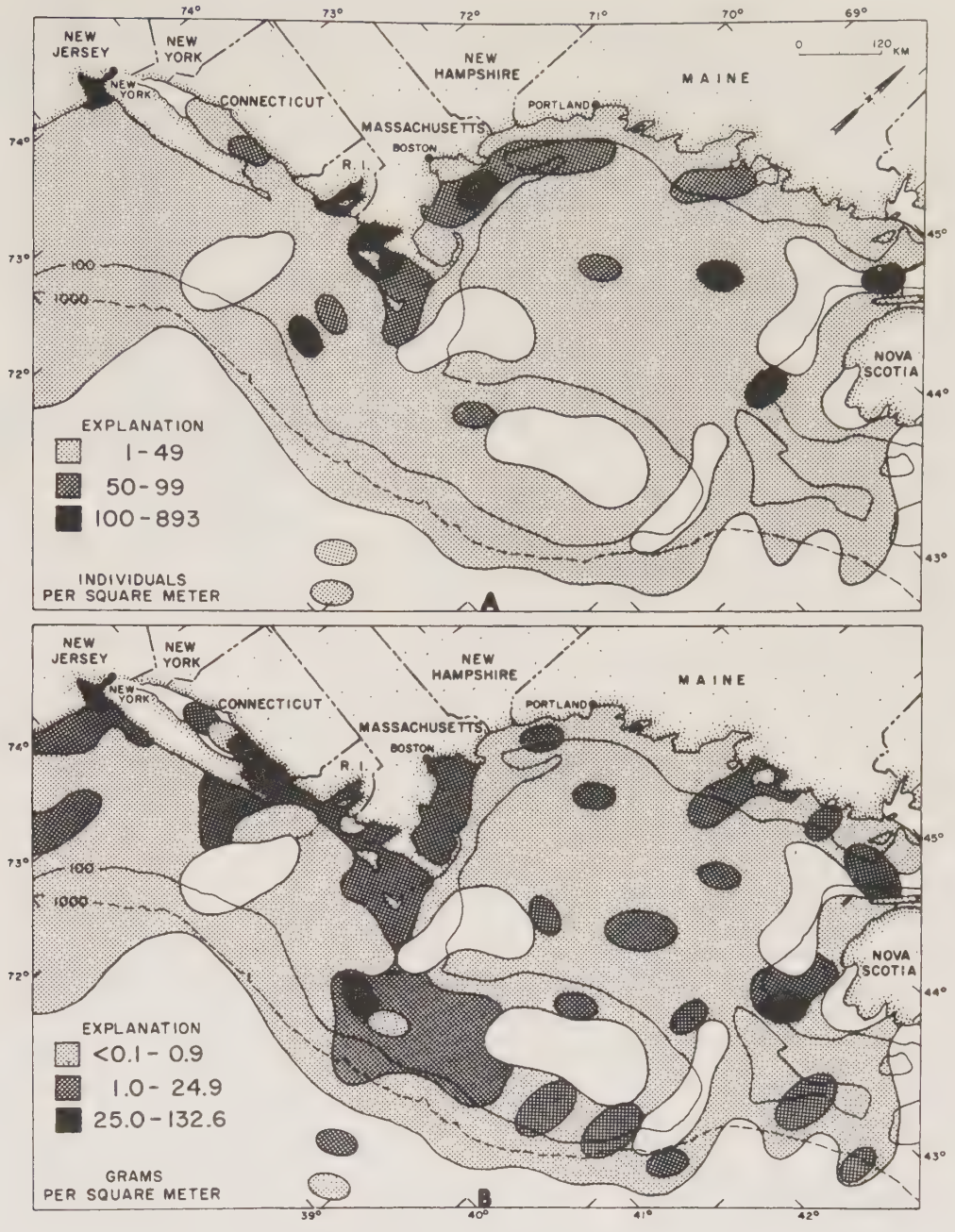


Figure 110
Density and biomass of Polyplacophora in relation to sediment organic carbon.



GASTROPODA

Figure 111

Geographic distribution of Gastropoda: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

In terms of biomass, the gastropods were most prevalent (3.3 g/m^2) in sand and gravel substates (Table 18; Fig. 114). They occurred in intermediate quantities (2.1 and 1.6 g/m^2) in shell and sand-silt. Low quantities (0.2 g/m^2) were found in till and silt-clay sediments.

Frequency of occurrence was high (83%) only in samples from shelly sediments (Table 20). In all other bottom types the occurrence of gastropods was quite uniform at a moderate (42 to 50%) level.

Relation to Water Temperature

The greatest quantities of gastropods, in terms of both density and biomass, occurred where the annual range in temperature exceeded 16°C (Tables 21, 23; Fig. 115).

Both measures indicated a trend of increasing abundance with increased range in temperature. Quantitative values for density were proportionally higher than those for biomass, but the percentage composition of the total fauna for both measures was moderately low (Tables 22, 24). With the exception of the two broadest temperature range classes (16°–19.9° and 20°–23.9°C), where relatively high densities (85 and 47 individuals/m^2, respectively) occurred, gastropod density was fairly uniform at a moderate level of about 10 to 15 individuals/m^2.

Gastropod biomass values generally paralleled those of density, but the trend of increased biomass with increased temperature range was more pronounced. The two largest biomasses (4.96 and 4.09 g/m^2) occurred in the two broadest temperature range classes. In all other temperature range classes the biomass was moderate (0.26 to 3.75 g/m^2) and fairly stable.

Frequency of occurrence of these organisms was moderately high and stable in all temperature range classes (Table 25). They varied only from 38 to 57%, with no obvious trends.

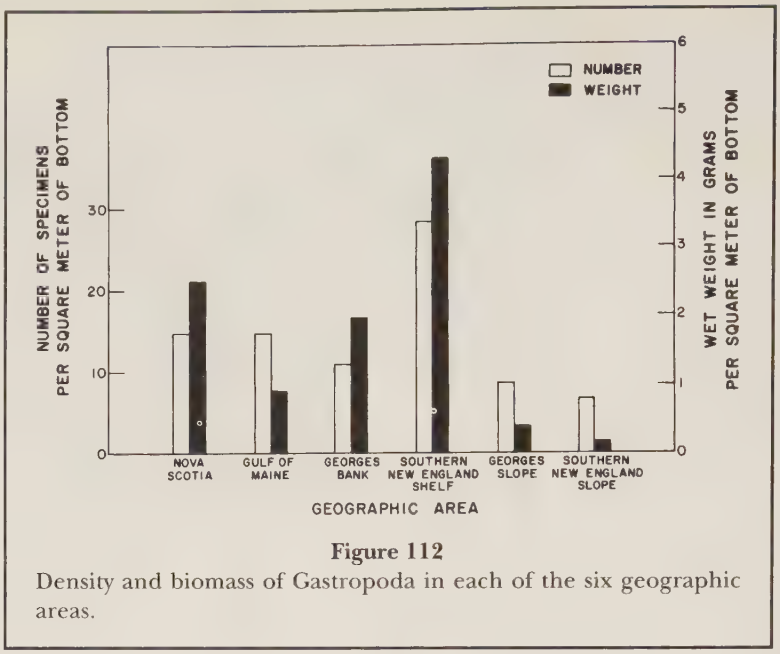


Figure 112
Density and biomass of Gastropoda in each of the six geographic areas.

Relation to Sediment Organic Carbon

Gastropods displayed a generally bimodal trend of increasing numerical abundance and biomass with increasing (to moderate levels) organic carbon content in the sediments (Tables 26, 28; Fig. 116). Average density ranged from a low of 2 individuals/m^2 in areas with no measurable organic carbon to a high of 45/m^2 in 1.5 to 1.9% organic carbon. The first peak (20/m^2) occurred in levels of 0.01 to 0.49% and the second in the 1.5 to 1.9% class. No gastropods were found where carbon content was greater than 3%.

Biomass values ranged from a low of 0.02/m^2 in the absence of organic carbon to a high of 10.42 g/m^2 in the 2.00–2.99% content class. The first peak in moderate biomass (3.8 g/m^2) occurred at levels of 0.01–0.49%. Biomass decreased significantly between 0.50 to 1.99% levels and rose dramatically to highest recorded biomass in the highest levels in which they were found.

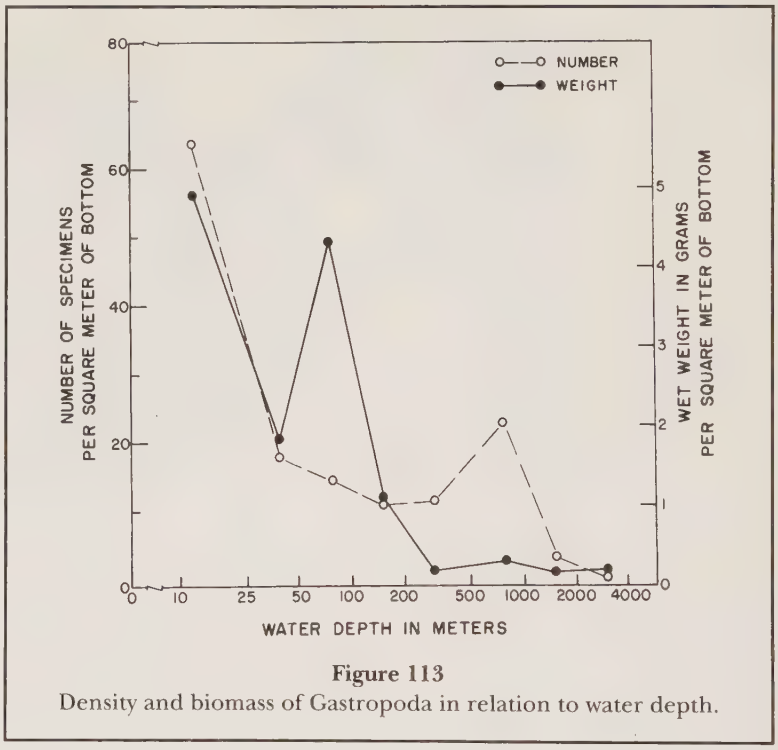


Figure 113
Density and biomass of Gastropoda in relation to water depth.

Frequency of occurrence ranged from 20 to 61% of the samples (Table 30). Lowest occurrence occurred at both extremes of carbon content, whereas fairly uniform occurrence occurred in the other content classes.

Bivalvia—Bivalvia were inordinately dominant in terms of wet weight, contributing 44.1% of the total biomass of the New England marine benthic fauna. In terms of number of individuals they provided 10.8% of the total (Table 3). Weight determinations included shells (see "Material and Methods"), but even if shells were excluded from weight measurements, the Bivalvia would still rank first in biomass. In number of individuals they rank third, after Amphipoda and Annelida.

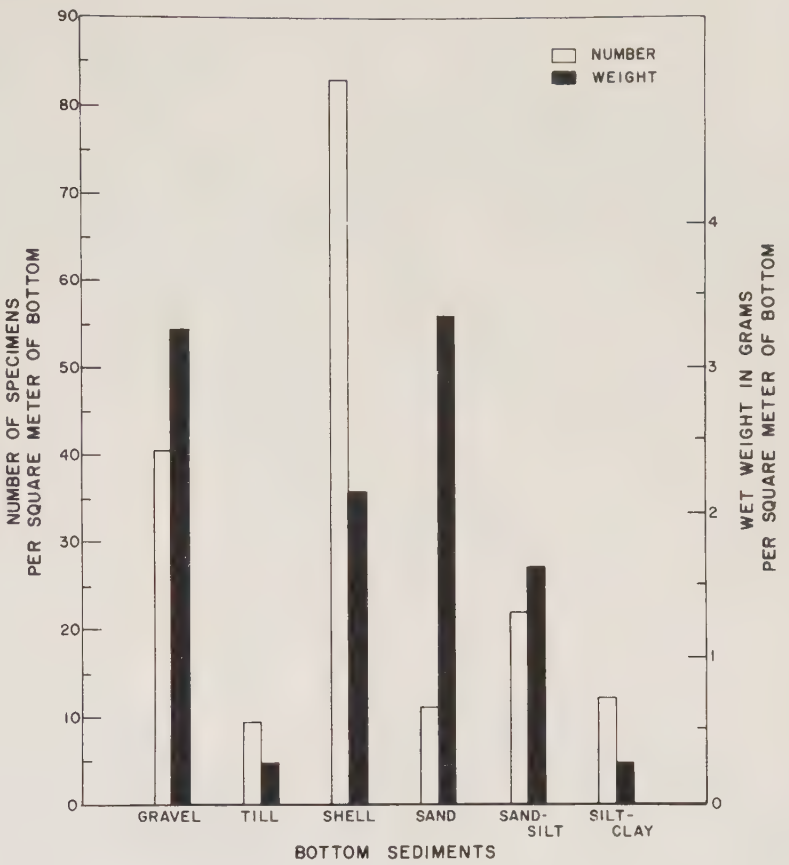


Figure 114
Density and biomass of Gastropoda in relation to bottom sediments.

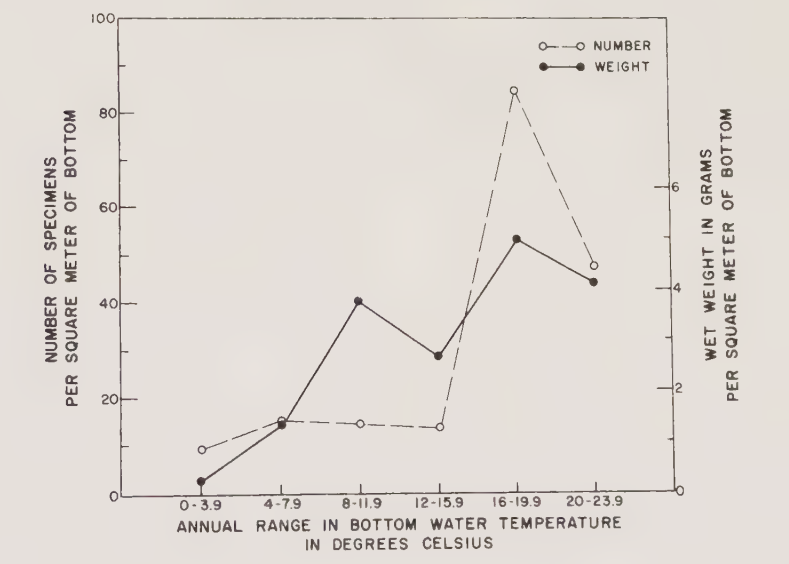


Figure 115
Density and biomass of Gastropoda in relation to the annual range of bottom water temperature.

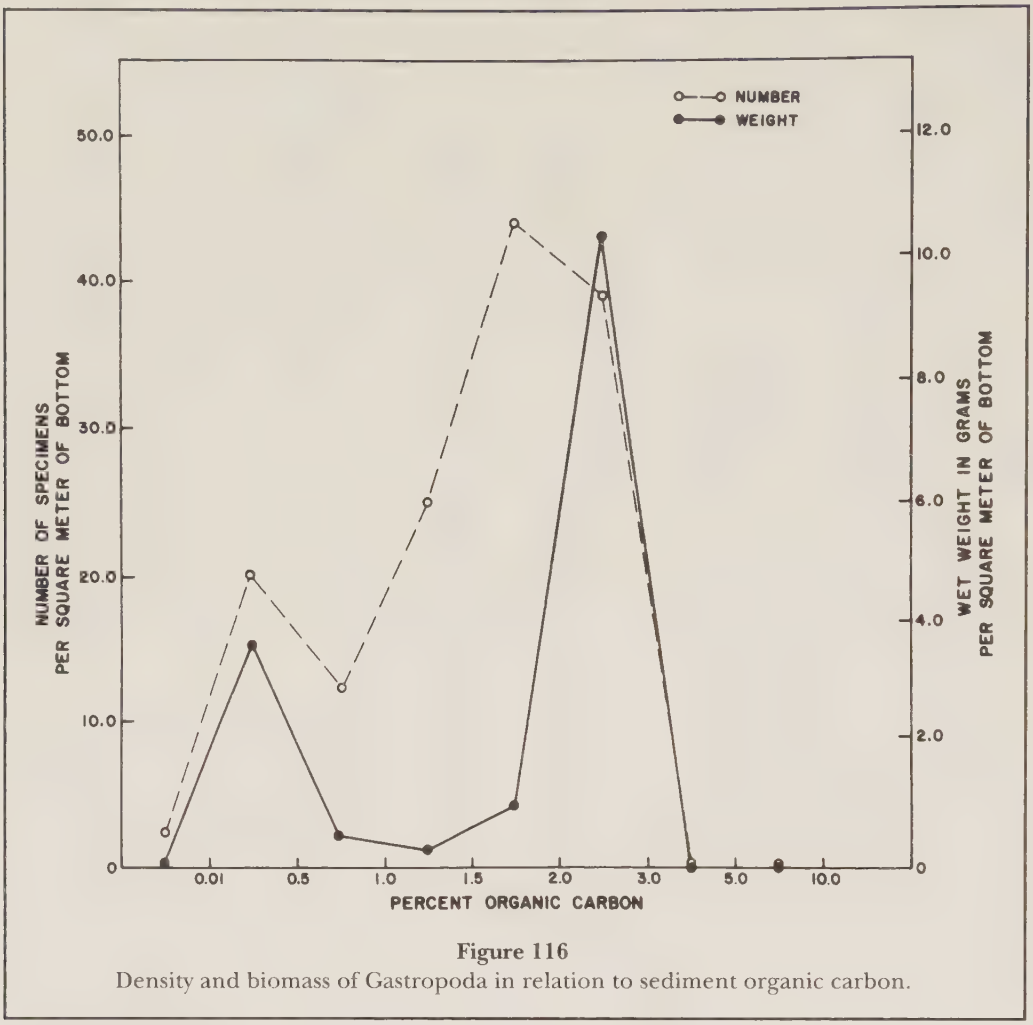


Figure 116
Density and biomass of Gastropoda in relation to sediment organic carbon.

Bivalvia were distributed throughout the entire area sampled in all water depths, sediment types, and temperature range classes. They were especially plentiful on the continental shelf where their average density commonly ranged from about 50 to 500/m^2. Biomass of bivalves averaged 100g/m^2 or more over a large portion of the continental shelf.

A rather wide variety of bivalve species occurs in this region, and it is estimated that more than 125 species were present in the samples (Theroux and Wigley, 1983). Some of the more common families represented were Astartidae, Veneridae, Mytilidae, and Nuculanidae.

Size of specimens ranged from roughly 15 cm for *Modiolus modiolus* and *Placopecten magellanicus* to about 3 mm for *Gemma gemma, Thyasira gouldi,* and other small forms. Large specimens occurred only in shallow and moderately shallow water, and in medium to coarse sediments, whereas small specimens were taken at all depths but mostly in fine-grained sediments.

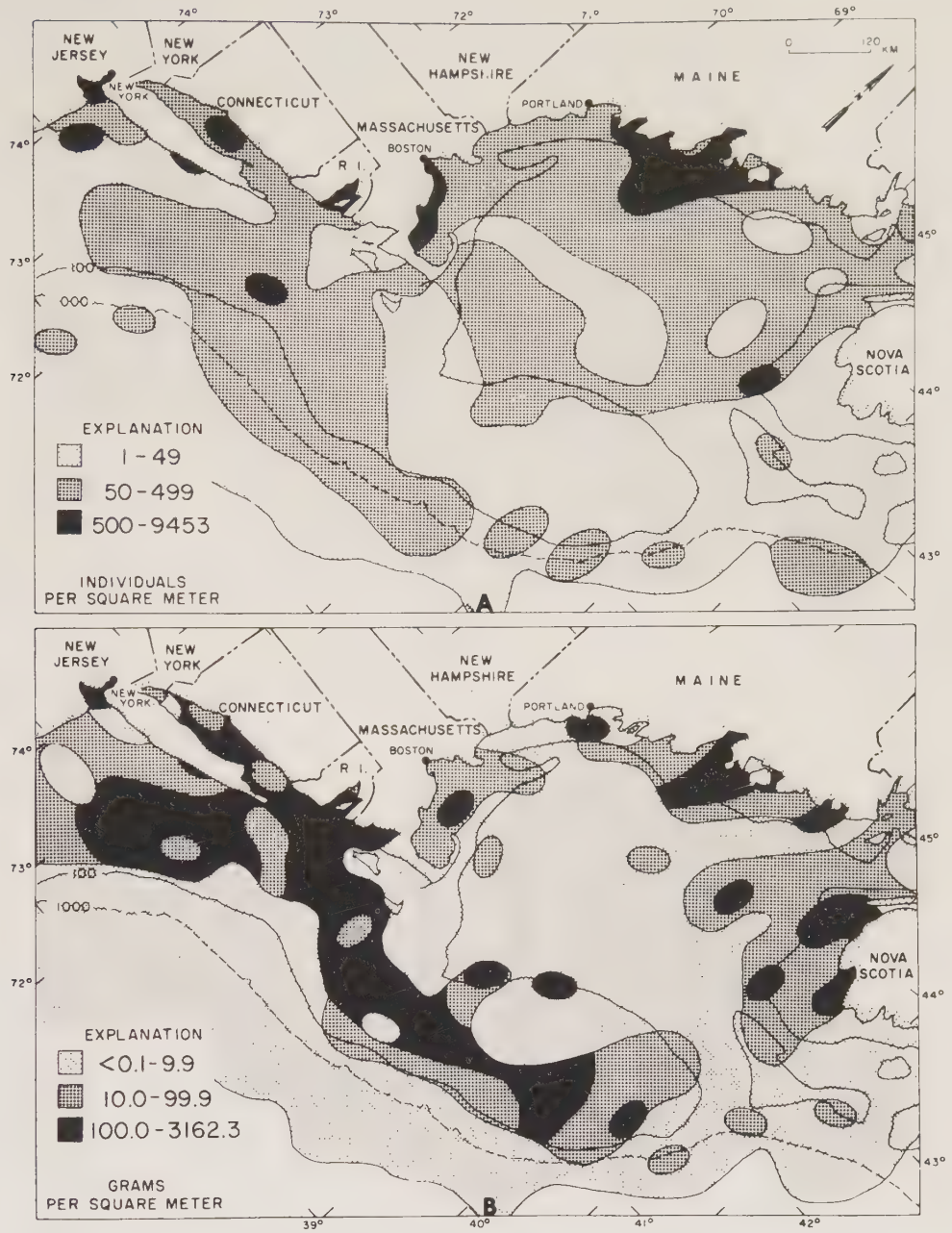
The color of bivalves in these collections ranged from white to blackish-brown. The most common colors were white, light gray, and various shades of brown or olive. No bright or vividly colored species were represented. Some of the more colorful forms were *Tellina, Thyasira ovata,* and some specimens of *Placopecten magellanicus.*

In addition to the importance of oysters, soft-shell clams, quahogs, surf clams, and scallops as food for man, the bivalves as a group are a major source of nourishment for many marine animals. Mammals, birds, fishes, and invertebrates all have members that prey heavily upon bivalves.

Bivalves occurred in 893 samples (83% of total). Their density averaged 163/m^2 and biomass averaged 81 g/m^2 (Table 5).

Geographic Distribution

Bivalves were distributed over the entire New England region (Fig. 117). Average densities per 20-minute unit area ranged from 1 to nearly 10,000 individuals/m^2. High densities (>500/m^2) were most common in nearshore areas. Moderate densities (50 to 500 individuals/m^2) occurred over extensive areas in the Gulf



BIVALVIA

Figure 117

Geographic distribution of Bivalvia: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

of Maine, on the Southern New England Shelf, and along the continental slope south of Georges Bank and Nova Scotia.

Bivalves ranked above all other benthic animals in terms of weight. Average biomass ranged as high as 3,162 g/m^2 in some 20-minute unit areas. High biomass values of bivalves occurred over broad expanses of both the inshore and offshore sections of the Southern New England continental shelf, in Great South Channel, on the southern half of Georges Bank, and in coastal areas of the Gulf of Maine.

Within the six standard geographic areas bivalves were most numerous (212 to 276 specimens/m^2, respectively) on the Southern New England shelf and in the Gulf of Maine (Table 6; Fig. 118). Densities were moderate in all other areas including Georges Slope and Southern New

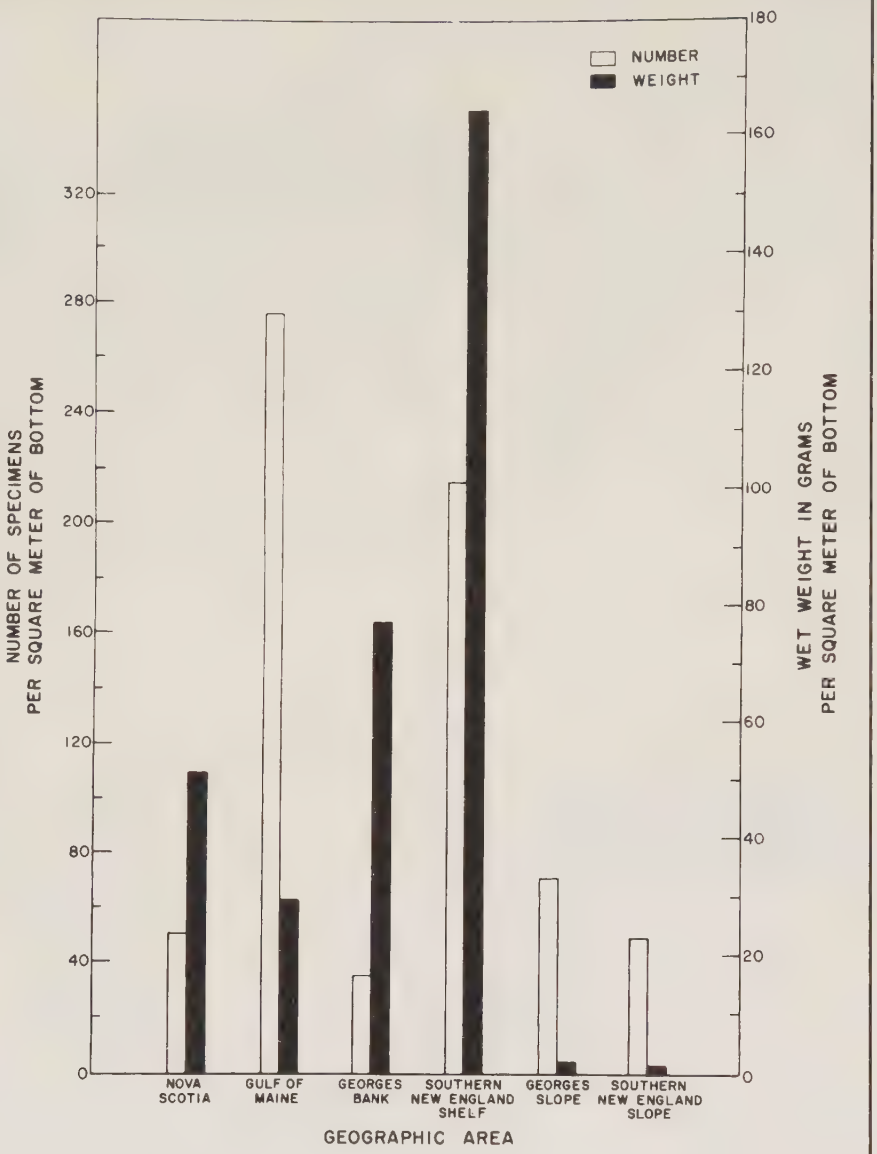


Figure 118
Density and biomass of Bivalvia in each of the six geographic areas.

England Slope. Lowest abundance ($34/m^2$) was on Georges Bank, but there the average size was greatest.

The biomass of bivalves was exceptionally high (averaged 166 g/m^2) on the Southern New England Shelf (Table 8; Fig. 118). Biomasses were moderate (30 to 77 g/m^2) in Nova Scotia, Gulf of Maine, and on Georges Bank. Average biomass of bivalves was smallest (1 to 2 g/m^2) in the Georges Slope and Southern New England Slope areas.

Frequency of occurrence was high in all areas, especially in the two slope areas where bivalves occurred in 89 and 94% of the samples (Table 10). Georges Bank had the lowest (64%) rate of occurrence. In all other areas the rate of occurrence was 80 to 89%.

Bathymetric Distribution

Bivalves were taken at depths from 3 to 3,820 m. They were common in all depth zones but occurred in greatest density (505 individuals/m^2) in shallow water (0 to 24 m) and diminished markedly with increasing water depth (Table 11; Fig. 119). In the deepest zone samples (2,000 to 3,999 m) their density was only $26/m^2$. The decrease in density was quite uniform; the major decrements in the trend were at about 25 m and 200 m.

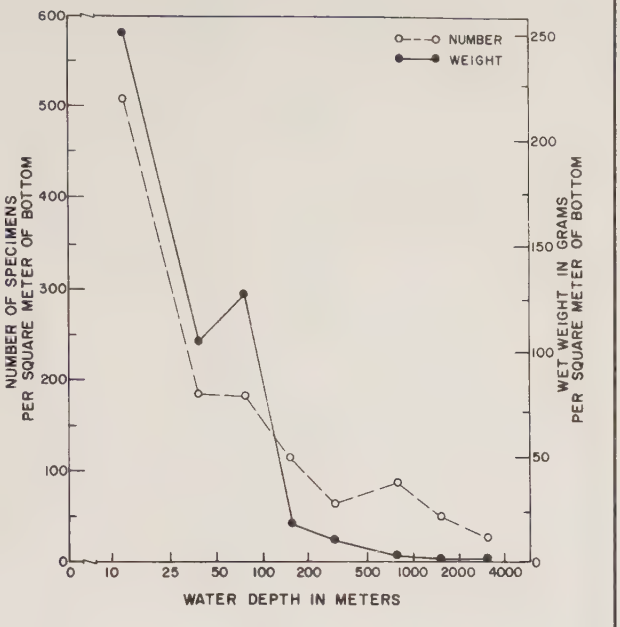

NUMBER
WEIGHT
NUMBER OF SPECIMENS PER SQUARE METER OF BOTTOM
WET WEIGHT IN GRAMS PER SQUARE METER OF BOTTOM
WATER DEPTH IN METERS
0 10 25 50 100 200 500 1000 2000 4000
600 500 400 300 200 100 0
250 200 150 100 50 0

Figure 119
Density and biomass of Bivalvia in relation to water depth.

Biomass of bivalves, as with density, was greatest (252 g/m^2) in shallow water and decreased sharply with increasing water depth (Table 13; Fig. 119). On the continental rise their biomass was only 0.4 g/m^2.

Bivalves were present in a high percentage of the samples from all depth classes. There was, however, a slightly higher rate (81 to 100%) of occurrence in deep water (greater than 500 m) than in shallow water, where the occurrence rate was 75 to 88% (Table 15). Other characteristics of the bivalve fauna in deep water are lower average density, lower maximum density, smaller average biomass, and smaller maximum biomass.

Relation to Sediments

Several clear trends were detected in the correlation between the quantity of bivalves and the type of bottom sediments they inhabited (Table 16; Fig. 120). Density was highest (330/m^2) in sediments composed of silt-clay and decreased as particle size increased, except in shell bottoms where the density of bivalves was moderately high (180/m^2). Gravels contained the lowest density (39/m^2).

An entirely different trend was observed for bivalve biomass (Table 18; Fig. 120). The largest quantities (117 to 165 g/m^2) were found in sediments of medium grain size. Smallest quantities (5 to 18 g/m^2) occurred in till and silt-clay. It should be noted that in four of the six sediment types, the biomass of bivalves accounted for over 42% of the total benthic biomass (Table 19). In shelly sediments they formed the exceptionally large proportion of 74% of the total fauna.

Bivalves were present in a high proportion of the samples in all sediment types. They occurred in all samples from shelly bottoms and in a particularly high percentage (91 to 92%) of the samples from fine-grained sediments (Table 20). Only a moderately high proportion of the samples from sand and gravel contained live specimens of bivalves.

Relation to Water Temperature

Bivalves occurred in significant quantities in all of the temperature range classes (Tables 21, 23; Fig. 121). Although the density and biomass exhibited a general tendency of increasing as the temperature range broadened, two major anomalies in this trend were observed in the two highest range intervals. The 16°–19.9°C class had a large biomass (334 g/m^2) and a moderate (252 individuals/m^2) density, indicating the presence of larger individuals than in other areas. Conversely, the 20°–23.9°C class had a high density (1,195 individuals/m^2) but a small biomass (84 g/m^2).

Bivalve biomass was unusually large (106 to 334 g/m^2) where the temperature range was moderate (8°–19.9°C) and was comparatively smaller in the low and high ranges (6.8 and 84 g/m^2, respectively).

Frequency of occurrence of bivalves was high and rather uniform (75 to 93%) among all temperature range classes (Table 25).

Relation to Sediment Organic Carbon

Bivalves were found in significant quantities in all organic carbon content classes except the highest (5.00+%). There was a well-defined positive correlation of increasing density with increasing organic carbon content (Table 26; Fig. 123). Density of bivalves rose from moderate levels (64/m^2) in the absence of organic carbon to high levels (1,120/m^2) where organic carbon content was between 3 and 5%. Bivalvia is the only taxonomic group showing such a well-defined trend in relation to sediment organic carbon. This trend corresponds to that shown for depth distribution, wherein higher bivalve densities occurred in the shallower estuarine and embayment waters that contained the highest levels of organic carbon.

Although the highest biomasses of bivalves (227 to 801/m^2) were found in the higher carbon content classes (3.00–4.99% and 2.00–2.99%, respectively) the relationship was not as well-defined as that for density (Table 28; Fig. 122). Moderately high biomass (128/m^2) also occurred in low carbon levels (0.01–0.49%). The other carbon content classes contained significantly lower biomasses.

Frequency of occurrence of bivalves in samples in the various organic carbon content classes was quite high

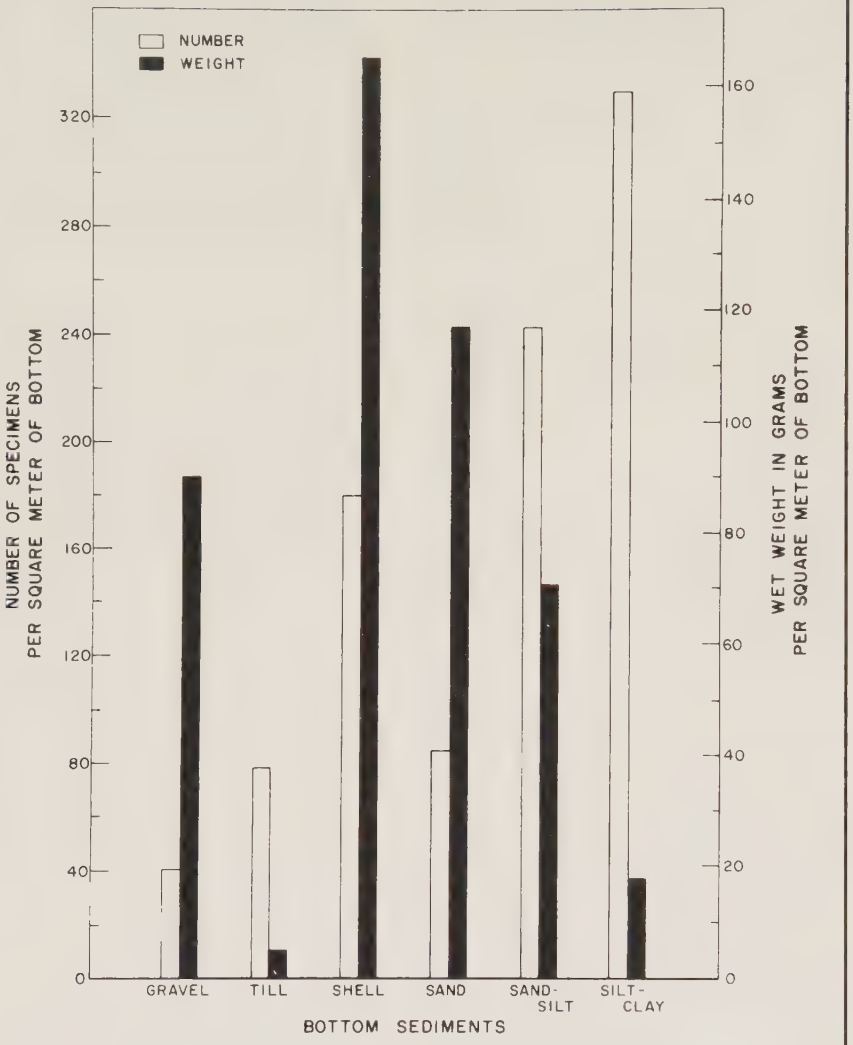


Figure 120
Density and biomass of Bivalvia in relation to bottom sediments.

and relatively uniform, ranging from 80 to 100% between the 0.00 and the 2.00–2.99% classes; the lowest occurrence (75%) was in the 3.00–4.99% class (Table 30).

Scaphopoda—Scaphopods constituted a minor component of the New England benthic fauna. They accounted for 0.2% of the number of animals and 0.3% of biomass in the total benthic fauna (Table 3). These samples included the first representative of the genus *Cadulus* known to occur in the Gulf of Maine (Wigley, 1966b). This same report postulated that the relatively warm high-salinity bottom water in the larger Gulf of Maine basins permitted scaphopods from the continental slope to inhabit deeper sections of the Gulf.

They are burrowing forms that most commonly inhabit medium to fine-grained sediments. The head and relatively large foot project from the anterior (larger) aperture of the shell. When buried in the sediment the anterior end of the shell faces downward and the posterior end is pointed upward. Scaphopods have planktonic eggs and free-swimming trochophoric larvae.

This group of mollusks is taxonomically small. Less than a score of species and one-half dozen genera are known from the New England region. Sizes of specimens in our samples ranged from about 1 to 6 cm in length.

Color of the shells was generally various shades of white, either uniformly white, or white with partial discolorations of yellow or brown, or occasionally black.

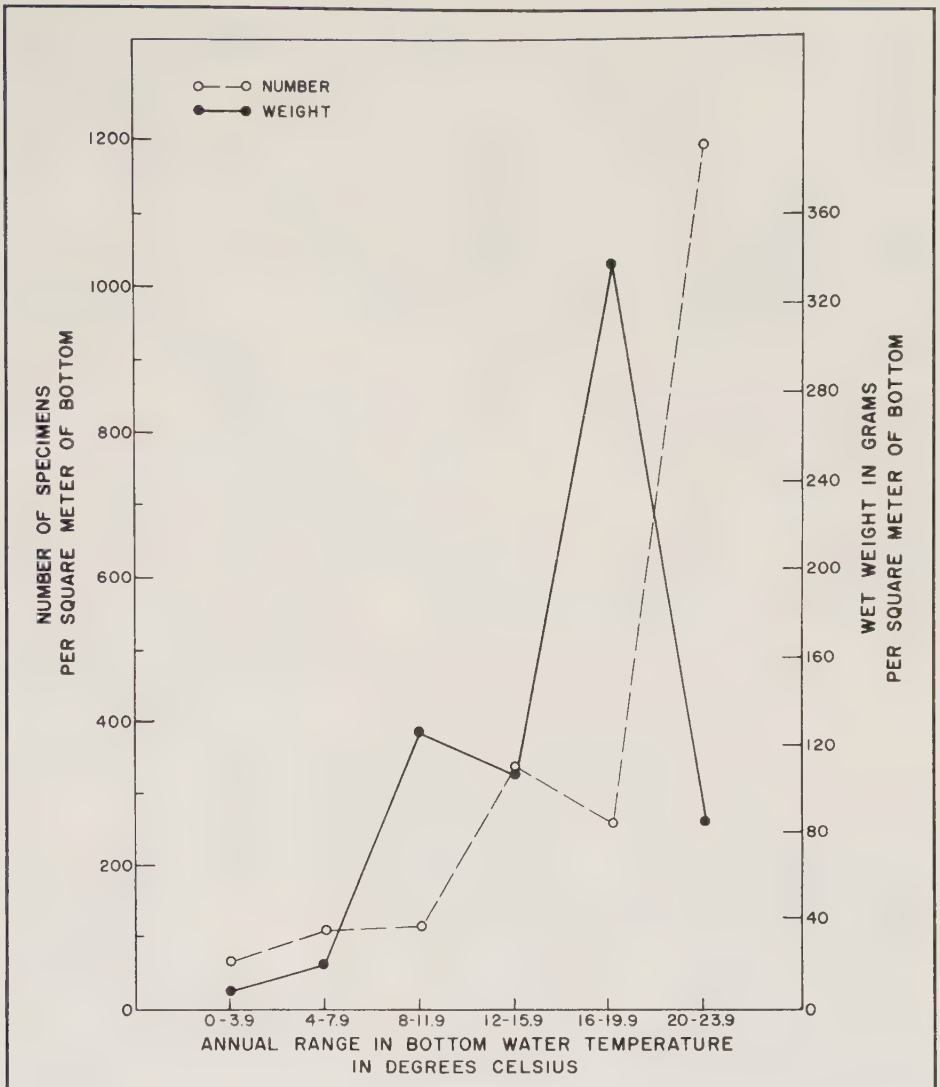


Figure 121
Density and biomass of Bivalvia in relation to the annual range of bottom water temperature.

Scaphopoda occurred in 218 samples (20% of total). Their density averaged 5.1/m^2 and biomass averaged 0.32 g/m^2 (Table 5).

Geographic Distribution

Scaphopods were present in moderately low densities (1 to 49 individuals/m^2) in large portions of the Nova Scotia and Gulf of Maine regions (Fig. 123). Farther south, with few exceptions, they were present only along the continental slope and the outer portion of the continental shelf. One area of relatively high density (50 to 106 individuals/m^2) was encountered in the north central part of the Gulf of Maine. The average biomass of scaphopods was moderately small in all areas, averaging less than 1 g/m^2 in more than 50% of their area of occurrence. Relatively large average biomasses (1 to 6 g/m^2) were common only in the northern part of the study area.

Within the six standard geographic areas scaphopods were most abundant (10 to 11 individuals/m^2) in the Nova Scotia and Gulf of Maine area (Table 6; Fig. 124). On Georges Slope and the Southern New England Slope their density was about 5/m^2. Lowest densities, approximately 1/m^2, were found on Georges Bank and the Southern New England Shelf.

The biomass of scaphopods was largest (0.7 to 1.0 g/m^2) in the northern areas, smallest (0.02 to 0.08 g/m^2) in the southern areas, and intermediate in intervening areas (Table 8; Fig. 124).

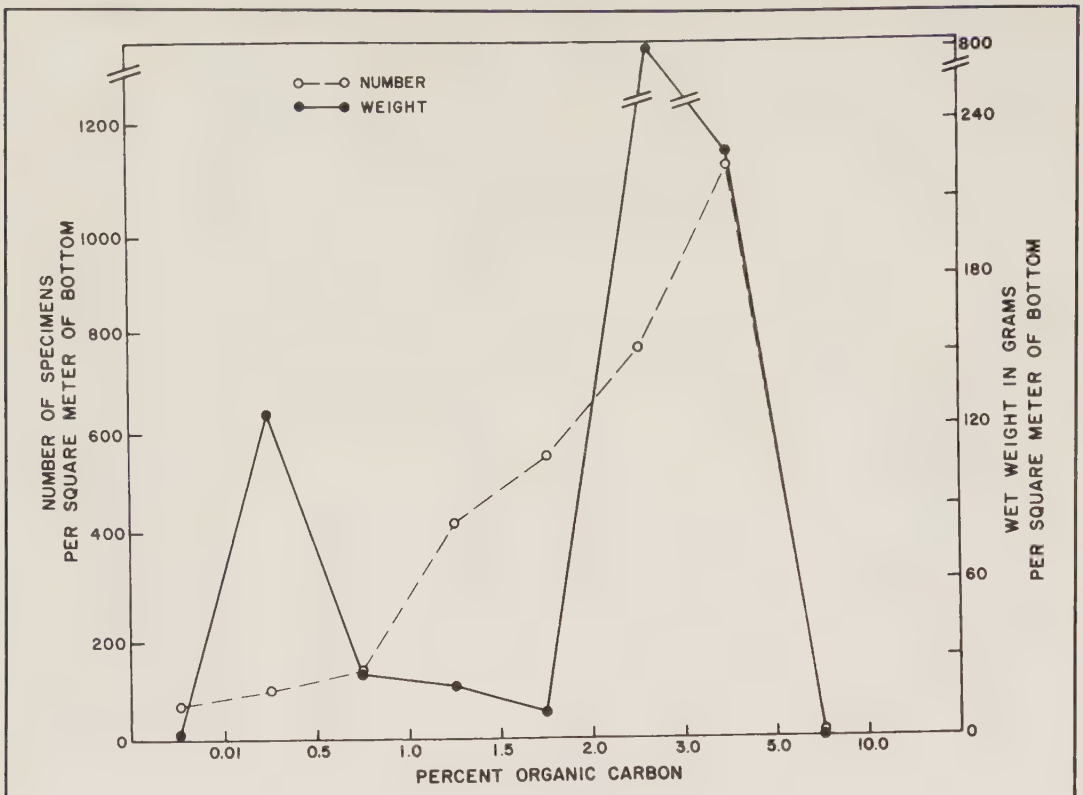


Figure 122
Density and biomass of Bivalvia in relation to sediment organic carbon.

A comparison of average density and average biomass in the various areas indicates that scaphopods are relatively large in Nova Scotia and on Georges Bank, and relatively small in the Southern New England Slope area.

Frequency of occurrence was low (4 to 7% of the samples) on Georges Bank and the Southern New England Shelf, and moderate (33 to 46% of the samples) in all other areas (Table 10).

Bathymetric Distribution

Scaphopods were taken at depths ranging from 19 to 2,329 m. They occurred in low density (0.1 and 0.2 individual/m^2) in both shallow water and deep water but were present in relatively high densities (10 to 14 individuals/m^2) in moderately deep water, 100 to 1,000 m (Table 11; Fig. 125). Increases and decreases in density about their center of abundance were surprisingly consistent and well correlated with changes in depth.

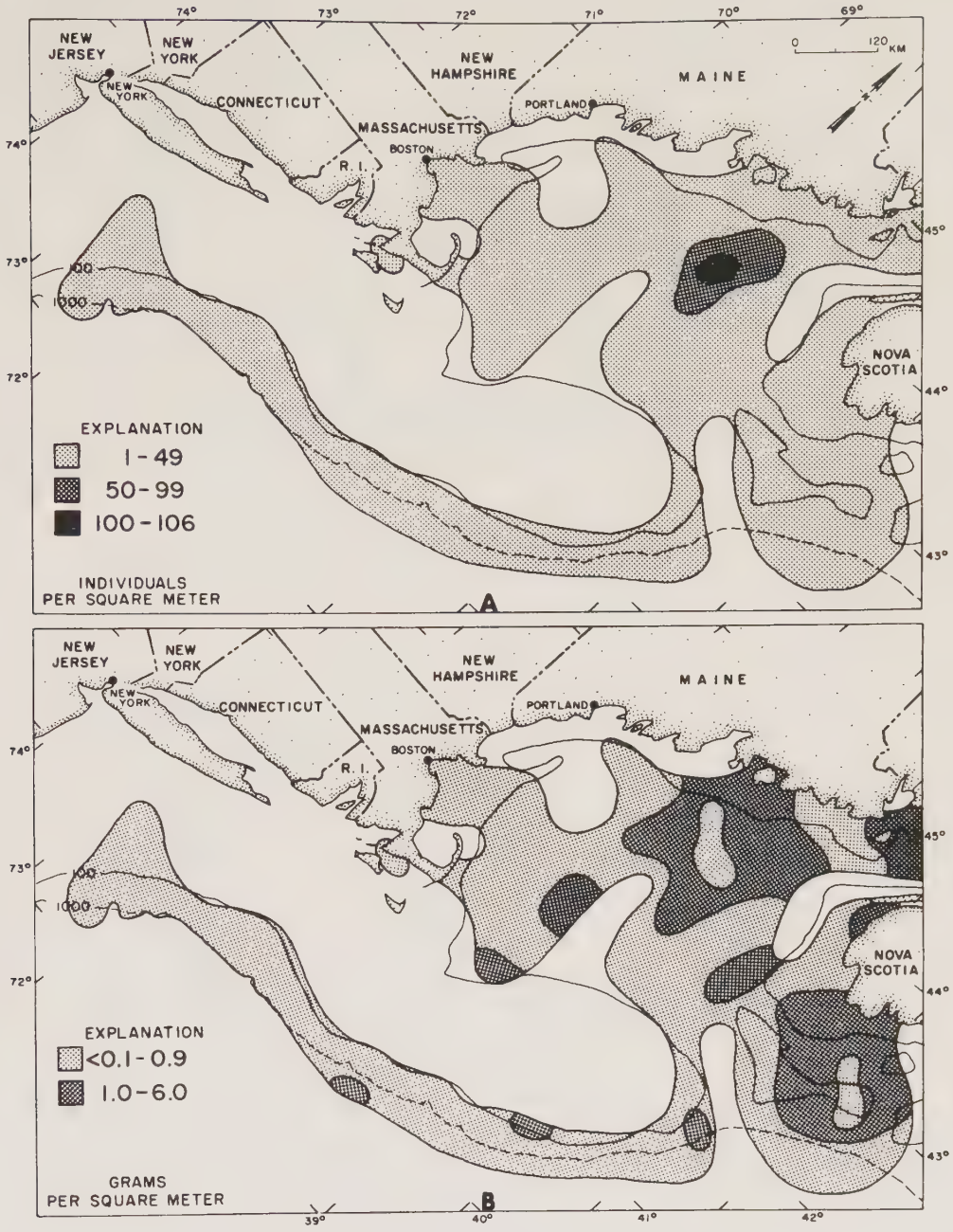
The biomass of scaphopods (Table 13; Fig. 125) was small (<1 g/m^2) in all depth classes, but changes in abundance relative to changes in water depth were similar to that described above for numerical density. Average biomasses in the shallowest and deepest bathymetric classes were <0.01 g/m^2. The average biomass was largest (0.17 to 0.98 g/m^2) in moderately deep water (100 to 2,000 m). Because of the small size and low density of this taxonomic group, it contributed a rather small share (1.6% or less) of the total benthic biomass in any depth class (Table 14).

Scaphopods occurred in a moderate share (35 to 59%) of the samples collected from depths between 100 and 2,000 m (Table 15). At depths both shallower and deeper, they occurred in less than 10% of the samples and in the two shallowest depth classes, they were present in only 1% of the samples.

Relation to Sediments

Scaphopods were present in all types of bottom sediments sampled, but were clearly more abundant (11 to 26 individuals/m^2) in the shelly and fine-grained sediments than in the coarse types (Table 16; Fig. 126). Sand and gravel bottoms yielded the lowest (1.8 and 2.0/m^2) densities. The percentage of the total faunal density composed of scaphopods was small (2.2% or less) in all types (Table 17).

Differences in biomass from one type of bottom to another were less pronounced than they were for density; however, the trend was the same (Table 18; Fig.



SCAPHOPODA

Figure 123

Geographic distribution of Scaphopoda: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

126). Relatively large biomasses were found in shell, till, and silt-clay sediments and small biomasses occurred in sand, sand-silt, and gravel. Scaphopods made up only a small portion (1.2% or less) of the total biomass in all bottom types (Table 19).

Frequency of occurrence of scaphopods was especially low (10 to 17%) in sand and gravel (Table 20). In shell, till, and other finer sediments they occurred in a moderate (30 to 46%) proportion of the samples.

Relation to Water Temperature

Scaphopods were most often found in the more stable environments where the temperature variations were small. Density and biomass of these organisms were

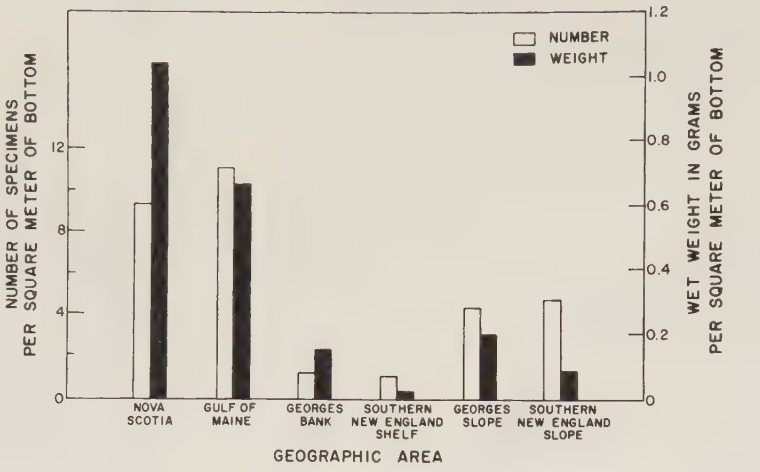


Figure 124
Density and biomass of Scaphopoda in each of the six geographic areas.

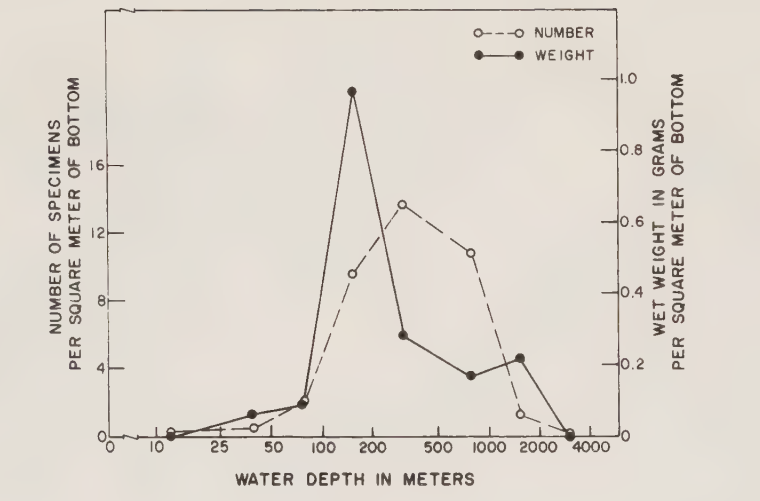


Figure 125
Density and biomass of Scaphopoda in relation to water depth.

greatest in the 4°–7.9°C range class and diminished steadily as temperature range broadened (Tables 21, 23; Fig. 127). None were found in the 20°–23.9°C class. Quantitative values for density ranged from 0.2 to 10.3 individuals/m^2 and for biomass from <0.01 to 0.92 g/m^2. In terms of both density and biomass they provided generally less than 2% of the total fauna (Tables 22, 24).

Scaphopods occurred in 2 to 37% of the samples in the temperature range classes in which they were found (Table 25). Frequency of occurrence was highest where the temperature range was small, and the frequency rate decreased as the temperature range expanded.

Relation to Sediment Organic Carbon

Scaphopods occurred where organic carbon content ranged from 0 to 2.99%. They were most abundant (12 to 13 individuals/m^2) in the two moderate carbon content classes 1.50–1.99 and 1.00–1.49%, respectively, and

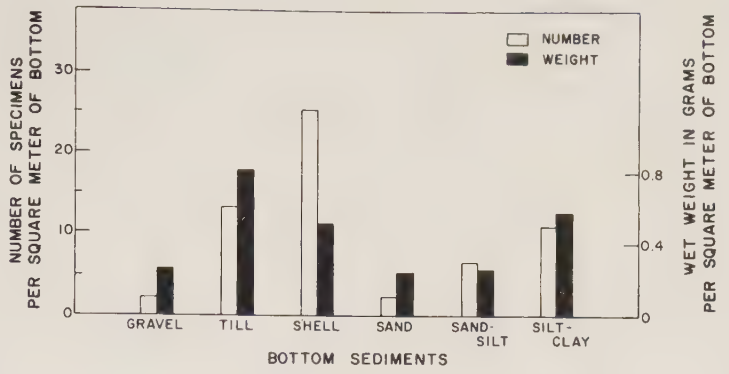


Figure 126
Density and biomass of Scaphopoda in relation to bottom sediments.

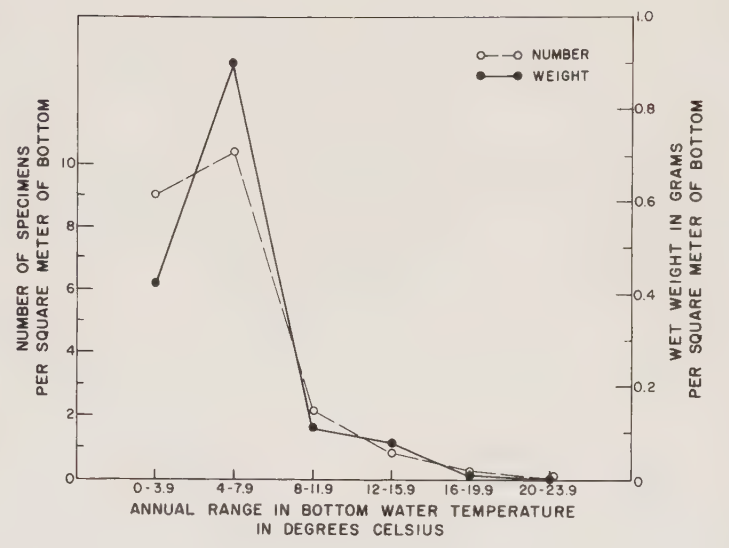


Figure 127
Density and biomass of Scaphopoda in relation to the annual range of bottom water temperature.

diminished in abundance where carbon content was both higher than and below those values (Table 26; Fig. 128).

Biomass peaked (0.48 g/m^2) in the 1.00–1.49% carbon content class with somewhat smaller amounts (0.31 g/m^2) in the 0.01–0.49% class (Table 28; Fig. 128); biomass in the other classes was fairly uniform ranging from 0.10 to 0.24 g/m^2.

Frequency of occurrence was moderately low in the 2.00–2.99% and 0.01–0.49% content classes (15 and 17%, respectively) but rose to moderate levels (20 to 32%) in samples in the other content classes (Table 30).

Cephalopoda—Representatives of the class Cephalopoda were not commonly encountered; they accounted for less than 0.1% of total biomass and density (Table 3). This apparent rarity is due primarily to sampling bias exemplified by the taxa represented in the samples. The class Cephalopoda contains some of the largest, most mobile, and most highly developed marine invertebrates known to science; further, many are semipelagic or pelagic in habit and are therefore severely undersampled by bottom grabs. The abundance and distribution of the commercially important squids inhabiting the study area in the order Decapoda, *Illex*

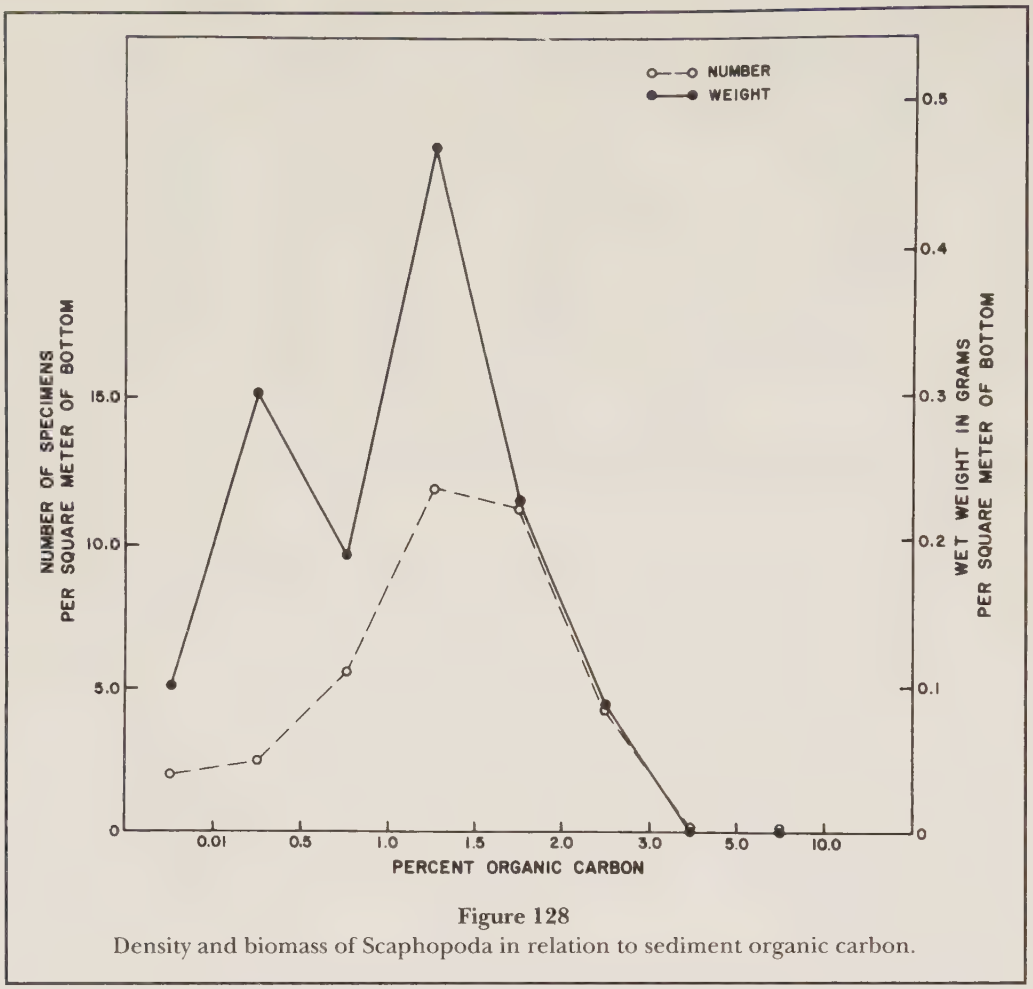


Figure 128
Density and biomass of Scaphopoda in relation to sediment organic carbon.

illecebrosus, and *Loligo pealei*, are well documented (Vovk, 1969; Tibbets, 1977; Lange, 1979, 1982; Wigley, 1982; Murray and Wigley[14] and others) in the fisheries literature but are not represented in our grab samples. Nautili and cuttlefish, two other orders of cephalopods that are wholly pelagic, are extremely rare in this region, which leaves only members of the order Octopoda, the octopi, which are almost wholly benthic in habit, and the smaller and more sedentary squids available to quantitative grab samplers. Thus the representation of cephalopods in our collections does not accurately characterize this portion of the molluscan fauna.

Our samples, 5 representing 0.5% of the total, contained a total of 376 individual cephalopods from 2 genera, *Octopus* sp. and *Rossia* sp. (Table 5). Their mean density was 0.4/m^2, and biomass averaged 0.01 g/m^2.

[14] Murray, H. E., and R. L. Wigley. 1968. Squid catches on three cruises of *Albatross IV*: cruise 63-5, July–August 1963; cruise 63-7, November–December 1963; cruise 64-1, January–February 1964. Bur. Comm. Fish, Biol. Lab., Woods Hole, Massachusetts Lab. Ref 68-12, 16 p. Unpubl. manuscript.

Geographic Distribution

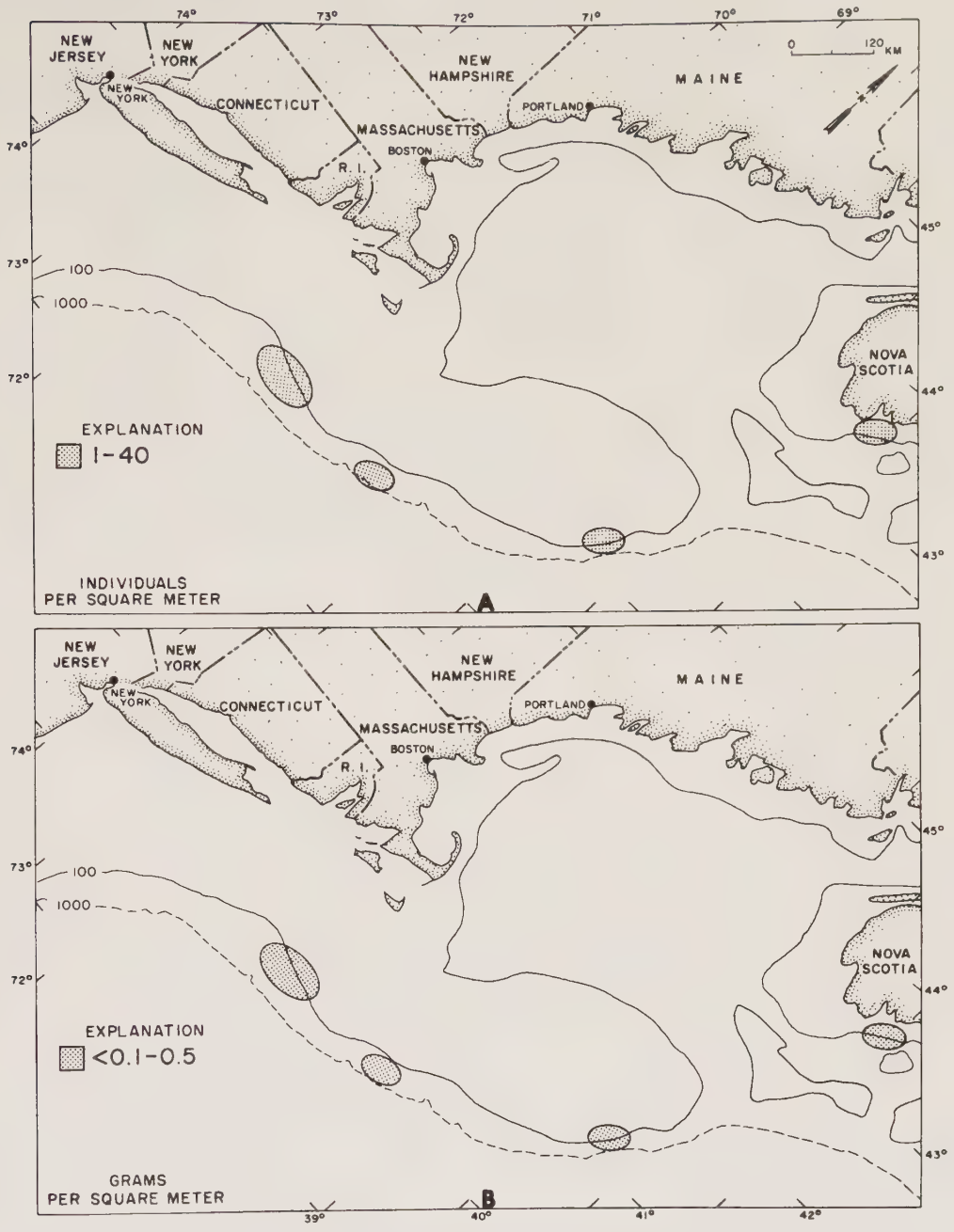
Cephalopods that were sampled occurred in low to moderate quantities (1 to 40 individuals/m^2, and <0.1 to 0.5 g/m^2) primarily along the offshore fringes of the study area at the shelf break and deeper from the northeast peak of Georges Bank westerly to south of Nantucket Shoals (Fig. 129). One inshore area, on the eastern Nova Scotian shelf, also yielded specimens of cephalopods.

Cephalopods occurred in all standard geographic areas but the Gulf of Maine in small quantities; mean densities ranged from <0.1 to only 1 individual/m^2, and mean biomass ranged from <0.01 to 0.01 g/m^2 (Tables 6, 8; Fig. 130).

Frequency of occurrence in the subareas was also low with <1 to only 2% of the samples containing specimens (Table 10).

Bathymetric Distribution

Cephalopods were taken at depths ranging from 114 to 320 m, placing them in two of our standard depth



CEPHALOPODA

Figure 129

Geographic distribution of Cephalopoda: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

range groupings (Tables 11, 13; Fig. 131). Highest mean density and biomass (1.5/m^2 and 0.03/m^2, respectively) occurred in continental shelf depths between 100 and 199 m, whereas at deeper depths, 200–499 m, mean density and biomass were significantly lower (0.1/m^2, and <0.01 g/m^2). Only 1% of the samples in each depth range grouping contained cephalopods (Table 15).

Relation to Sediments

Cephalopods were found only in gravel, sand, and sand-silt sediments. Average density was only <0.1/m^2 in both gravel and sand but was 1.7/m^2 in sand-silt substrates; average biomass, although low, increased with decreasing particle size ranging from <0.01 to 0.02 g/m^2 (Tables 16, 18; Fig. 132).

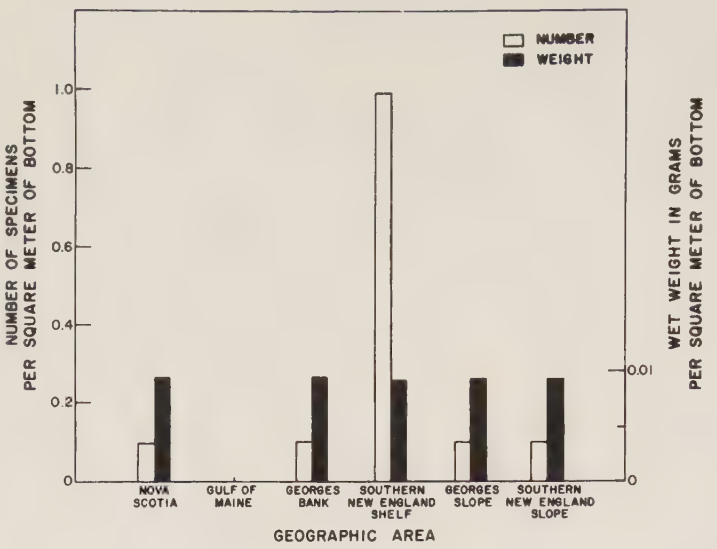


Figure 130
Density and biomass of Cephalopoda in each of the six geographic areas.

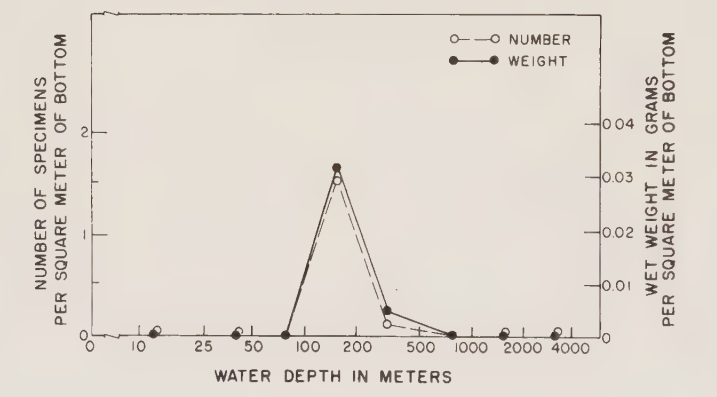


Figure 131
Density and biomass of Cephalopoda in relation to water depth.

Frequency of occurrence was low with only 1% of the samples in each of the three sediment types containing specimens (Table 20).

Relation to Water Temperature

Cephalopods were found only where the annual range in temperature was less than 12°C. Density showed a positive correlation with increasing temperature range from <0.1 individuals/m^2 in the narrowest (0–3.9°C) range to 1.1 individuals/m^2 in the broadest (8–11.9°C) range in which they occurred (Table 21; Fig. 133).

Biomass was stable (0.02 g/m^2) in the ranges between 4° and 11.9°C, and low (<0.01 g/m^2) in the narrowest range (Table 23; Fig. 133).

Less than 1% of the samples in the 0–3.9° and 8–11.9°C range groupings contained cephalopods, whereas 2% of the samples in the 4–7.9°C grouping yielded specimens (Table 25).

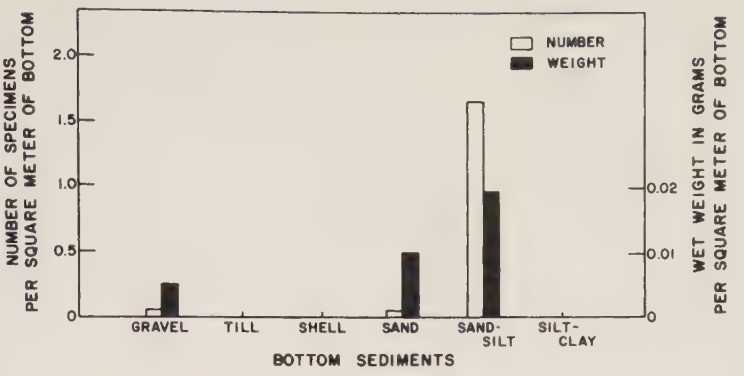


Figure 132
Density and biomass of Cephalopoda in relation to bottom sediments.

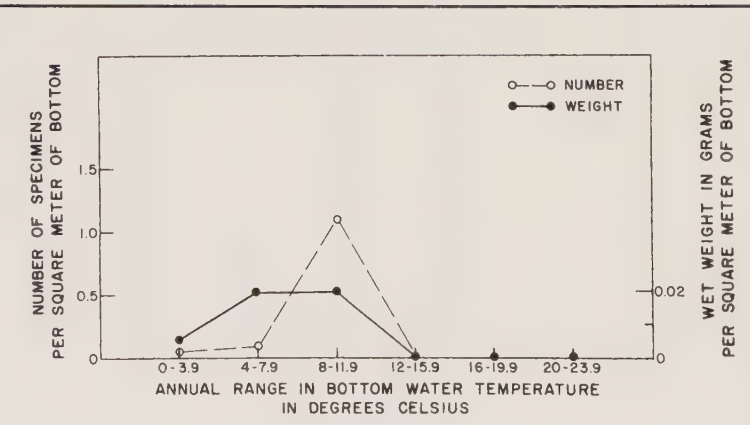


Figure 133
Density and biomass of Cephalopoda in relation to the annual range of bottom water temperature.

Relation to Sediment Organic Carbon

Cephalopods occurred only where organic carbon content ranged between 0.01 and 0.99%. Highest density (2.1 individuals/m^2) and biomass (0.03 g/m^2) occurred in sediments with between 0.5 and 0.99% organic carbon; significantly lower quantities of both measures occurred at levels between 0.01 and 0.49% (Tables 26, 28; Fig. 134).

Frequency of occurrence of cephalopods in the samples was only 1% in each of the content classes into which they were grouped (Table 30).

Arthropoda

Representatives of the phylum Arthropoda in the New England region, members of the classes Arachnida, Pycnogonida, and Crustacea, contribute significantly to both measures of abundance. Among the nine orders of Crustacea inhabiting the region (see Table 4), Amphipoda is the overall dominant taxon in terms of density, contributing slightly over 43% of the total number of specimens; this is the same as their ranking in the Middle Atlantic Bight (Wigley and Theroux, 1981). The classes Arachnida and Pycnogonida and the nine orders of class Crustacea will be discussed separately below. In keeping with the phylogenetic order of treatment, the figures relating to Arthropoda (Figs. 135–139) are presented here, but the detailed discussion of the phylum, represented almost wholly by the class Crustacea, will be presented in the section "Dominant Components of the Macrobenthos" below.

Pycnogonida—The class Pycnogonida, a relatively small group of marine arthropods containing about 600

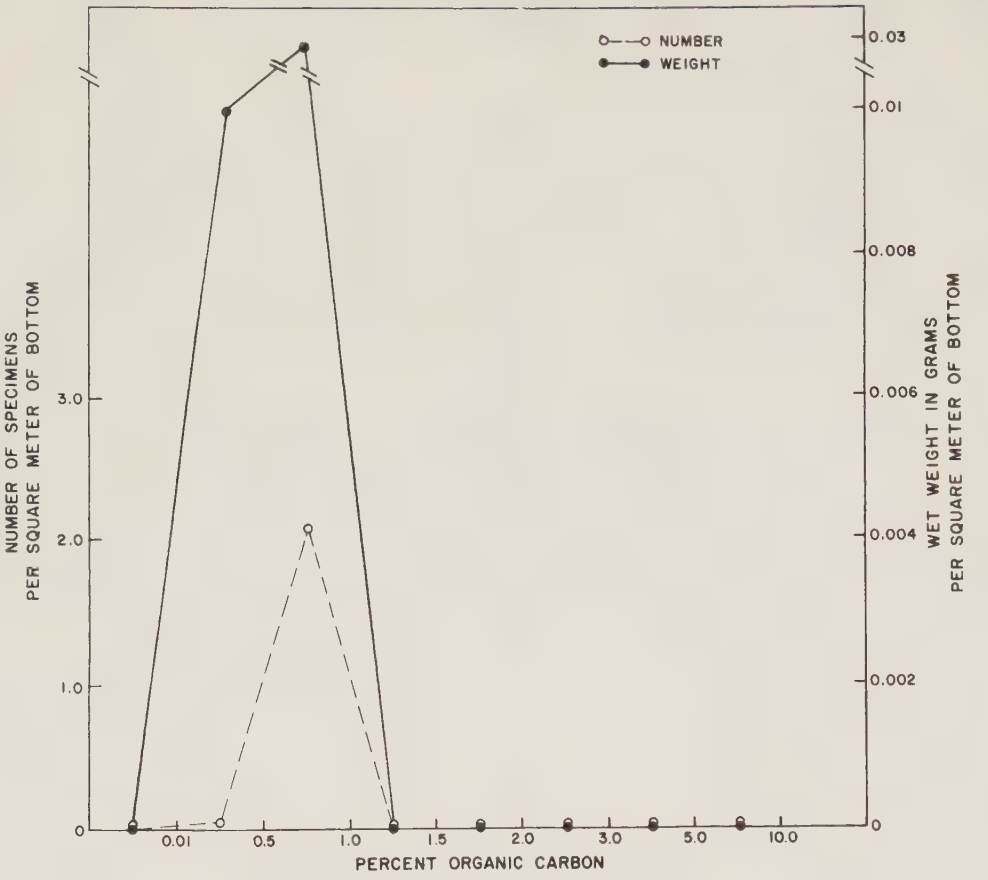


Figure 134
Density and biomass of Cephalopoda in relation to sediment organic carbon.

known species (Barnes, 1974), is commonly referred to as sea spiders. These organisms are found throughout the world ocean from the Arctic to the Antarctic and are considered to be common in occurrence. Most species prefer cold waters, and although some do swim, most are bottom dwellers and feed on hydroids, bryozoans, soft corals, anemones, and sponges. The sexes are separate and the males brood the developing eggs on specialized oviferous legs. They are for the most part small, ranging in length from 1 to 10 mm; however, a few species are much larger with body lengths of more than 6 cm and leg spans to 75 cm. They are found at nearly all depths but many species are littoral in habits. Color tends to be drab, but some pycnogonids are green and a few deepwater species are red.

Sea spiders were not very abundant in the study area, contributing less than 0.1% to total biomass and density (Table 3). In spite of this low abundance, a total of 10 species were identified from our samples (see Table 4). They ranged in depth from 18 to 1,420 m and were mostly 5 to 15 mm in size, with a few to 25 mm in length. Specimens ranged in color from flesh colored to dark tan and light brown.

Pycnogonids occurred in 25 samples (2.3% of total) which yielded a total of 369 individuals; mean number was 0.3/m^2 and biomass 0.01 g/m^2 (Table 5).

Geographic Distribution

The distribution of pycnogonids was quite patchy in the New England region, exhibiting inshore and offshore components (Fig. 140). The inshore component was composed of isolated patches of low density (1–9/m^2) and low biomass (<0.1–0.9 g/m^2) on the Nova Scotian shelf and inshore Gulf of Maine and in Long Island Sound. Patches of moderate density (10–49/m^2), but low biomass, were located at the entrances to the Bay of Fundy and Long Island Sound.

The offshore component contained patches of low density and biomass on Browns Bank, the Western Basin of the Gulf of Maine, and the periphery of Georges

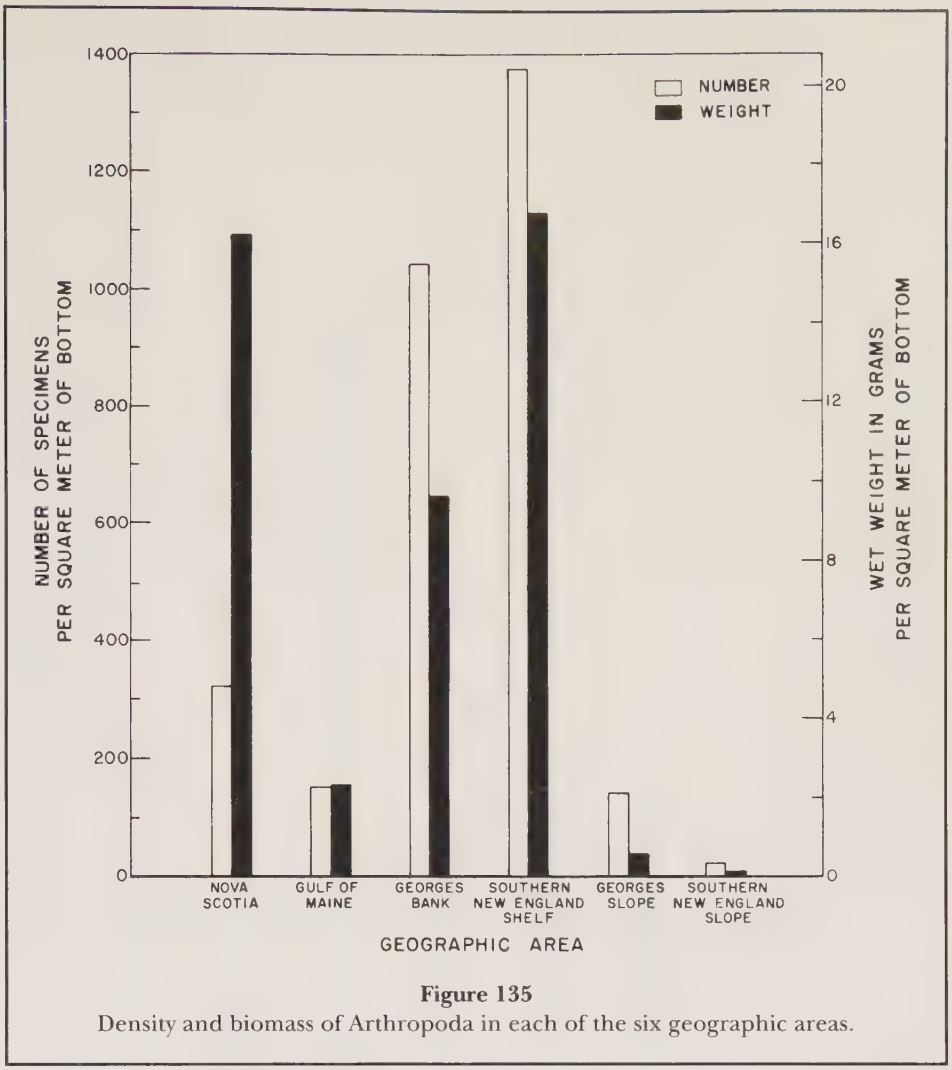


Figure 135
Density and biomass of Arthropoda in each of the six geographic areas.

Bank out onto Georges Slope. One patch of moderate density was located in Great South Channel.

Among the standard geographic areas, sea spiders were found in all but the Southern New England Slope. The shallow-water shelf areas, Nova Scotia, Southern New England Shelf, and Georges Bank, yielded higher mean densities (0.8–0.3/m^2) than the deeper Gulf of Maine and Georges Slope localities (Table 6; Fig. 141).

Mean biomass showed a diminishing trend from northeast to southwest, ranging from 0.02 to <0.01 g/m^2 (Table 8; Fig. 141).

Frequency and of occurrence was highest in Nova Scotia and on Georges Slope and lower in the other subareas (Table 10).

Bathymetric Distribution

Pycnogonids were absent in the 200–499 m and 2,000–3,999 m depth zones but present in small quantities in the other zones. Mean densities were highest (0.6/m^2) in the two zones between 0 and 49 m depth and diminished as depth increased (Table 11; Fig. 142). Lowest density (0.1/m^2) occurred in the deepest depth zone that they occupied (1,000–1,999 m).

Biomass of pycnogonids was low in all depth zones in which they occurred, ranging from <0.01 to only 0.03 g/m^2 (Table 13; Fig. 142). The highest biomass was in the 100–199 m depth zone.

Frequency of occurrence of sea spiders in samples was fairly uniform in most depth zones, ranging from 2 to 4%; however, 9% of samples in the 500–999 m zone contained specimens (Table 15).

Relation to Sediments

Shell is the only sediment type in which pycnogonids were not found. They were most prevalent (by a wide margin) in both measures of abundance in gravel, where

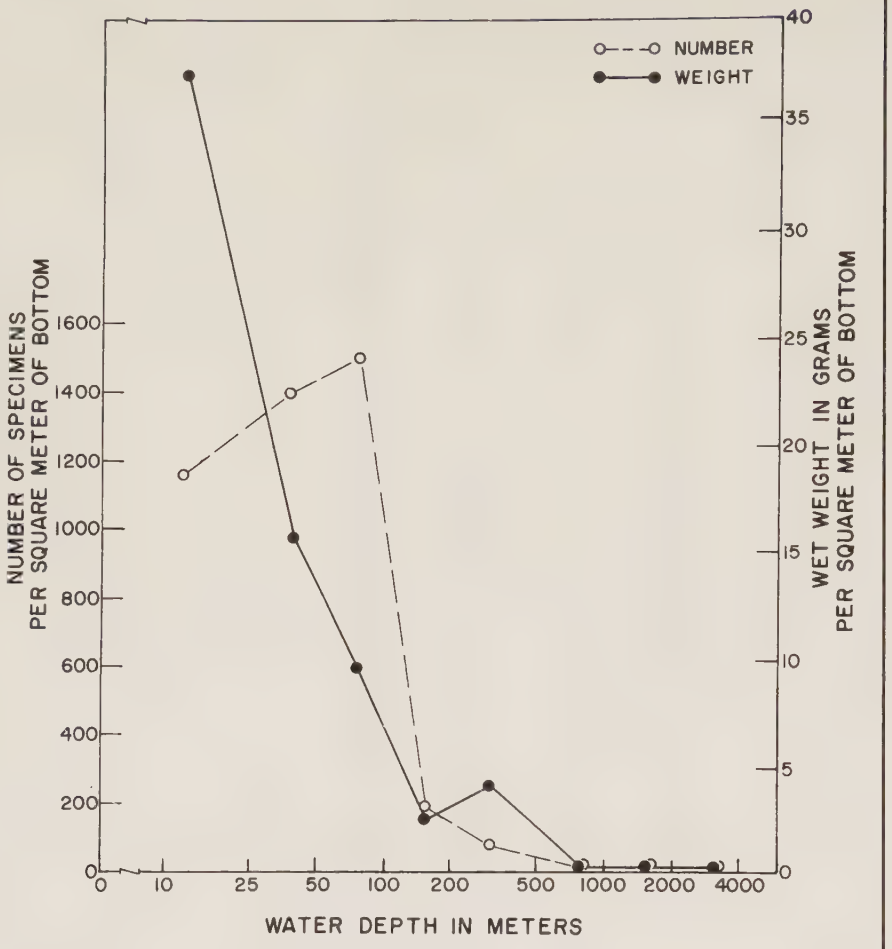


Figure 136
Density and biomass of Arthropoda in relation to water depth.

mean density and biomass were 2.1/m^2 and 0.05 g/m^2, respectively. Density and biomass in all other sediment types were significantly lower, 0.1/m^2 and <0.01 g/m^2, respectively (Tables 16, 18; Fig. 143).

Frequency of occurrence, as might be expected, was greatest in gravel (11% of samples), intermediate (5%) in till, and low (1%) in the other sediment types (Table 20).

Relation to Water Temperature

Sea spiders occurred in all temperature range classes. In terms of mean density there was a wide disparity in the quantities contained; the broadest temperature range (20–23.9°C) contained from 2 to 15 times more individuals (1.5/m^2) than any other range class, which had ranges from 0.1 to 0.7/m^2 (Table 21; Fig. 144).

Biomass was more evenly distributed among the different temperature range classes. However, the broadest temperature range did not contain the highest mean biomass (only 0.01 g/m^2), as it did density. The highest mean biomass occurred in the 4–7.9°C range class which contained 0.03 g/m^2. Mean biomass in the other temperature range classes was 0.01 g/m^2 or less (Table 23; Fig. 144).

Frequency of occurrence of pycnogonids in the samples in the various temperature range classes was rather uniformly low, ranging from 1 to 4%, with the highest incidence occurring in the two range classes that yielded the highest density and biomass (Table 25).

Relation to Sediment Organic Carbon

Pycnogonids were restricted to areas of low and moderate levels of organic carbon content, being found where values were between 0.01 and 1.49%. Mean density decreased from 0.4 to 0.1/m^2 as organic carbon con-

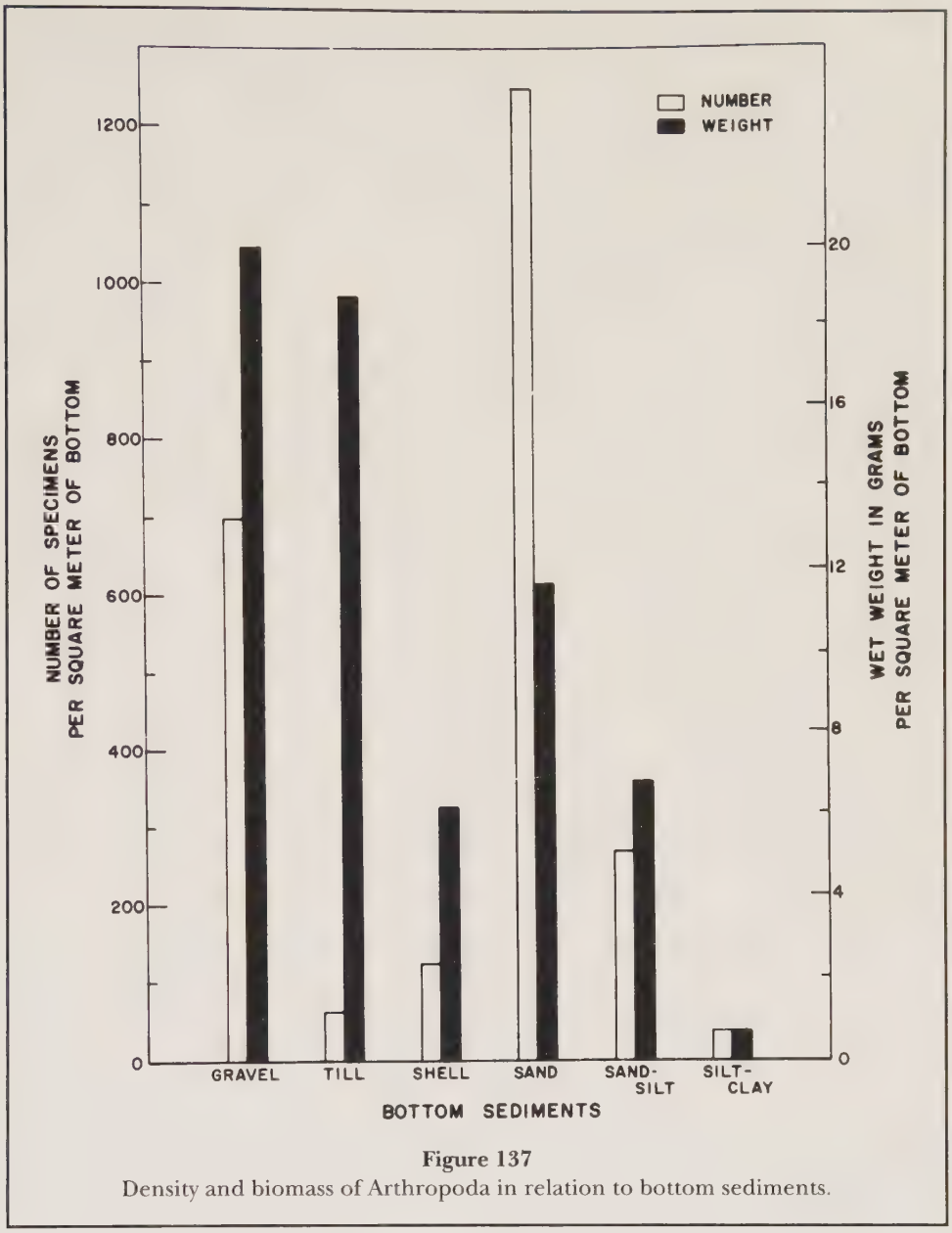


Figure 137
Density and biomass of Arthropoda in relation to bottom sediments.

tent increased, but mean biomass was fairly uniform, between 0.01 and <0.01 g/m^2 (Tables 26, 28; Fig. 145).

Frequency of occurrence of pycnogonids in samples also diminished as organic carbon content increased, ranging from 3 to 1% (Table 30).

Arachnida—One specimen of the class Archnida, order Acarina, family Halicaridae (water mite) was collected during the course of this study. This specimen was taken at station 1130, located at a depth of 86 m on the northeastern edge of Georges Bank. Sediment at this location was sand, and the temperature range was between 4° and 7.9°C.

Because of the small size of members of the family Halicaridae, only a very small proportion of them (the largest specimens) are components of the macrobenthos.

Adjusted statistics for this group are contained in Tables 3 and 5 for overall faunal relationship and in Tables 6 through 30 for relationships to the considered parameters.

Crustacea—The class Crustacea in the New England region contains representatives from nine orders, each of which will be discussed separately below. At least three of these orders, Amphipoda, Cumacea, and Cirripedia, rank as dominant components of the macro-

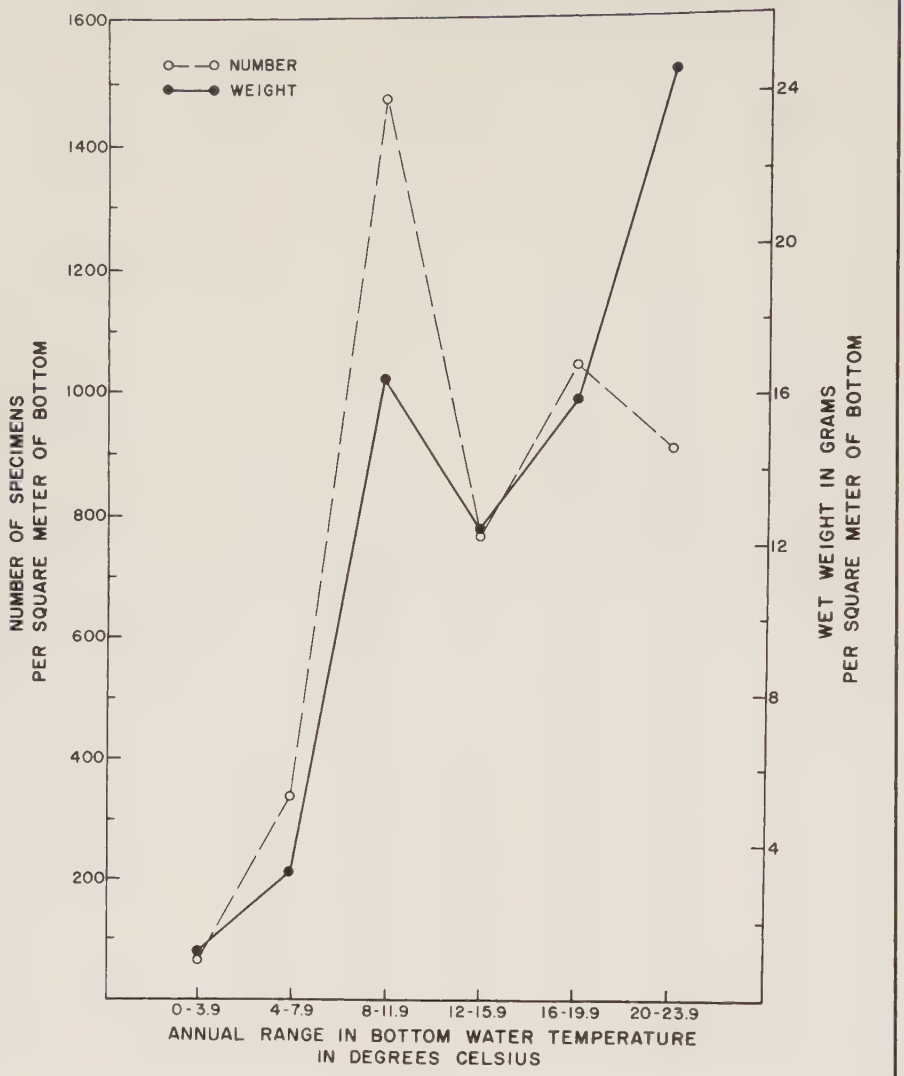


Figure 138
Density and biomass of Arthropoda in relation to the annual range of bottom water temperature.

benthic invertebrate fauna in terms of numerical density. Amphipoda, in particular, contributes an overwhelming majority of individuals (43%) to total faunal density, 1.5 times as many as the second dominant taxon, Annelida (28%) (Table 3). Cumacea and Cirripedia each contributed over 1.5% of total numerical density.

Detailed analysis of this class as a whole will appear below, along with the other dominant taxa, in the section "Dominant Components of the Macrobenthos." Figure 146, which shows the distribution of density and biomass of Crustacea, however is included here so as not to create disorder in the phylogenetic arrangement of the figures.

Ostracoda—Because of the small size of most members of this group, only a small proportion were retained by the processing techniques used in this study. Specimens in our samples were approximately 1 to 2 mm in length. The vast majority of ostracods inhabiting the sediments of this region, however, were smaller than this and as such belong to the meiofaunal realm not sampled in this study. Except for references to the literature, our comments here pertain only to the very largest species that occur in the New England region.

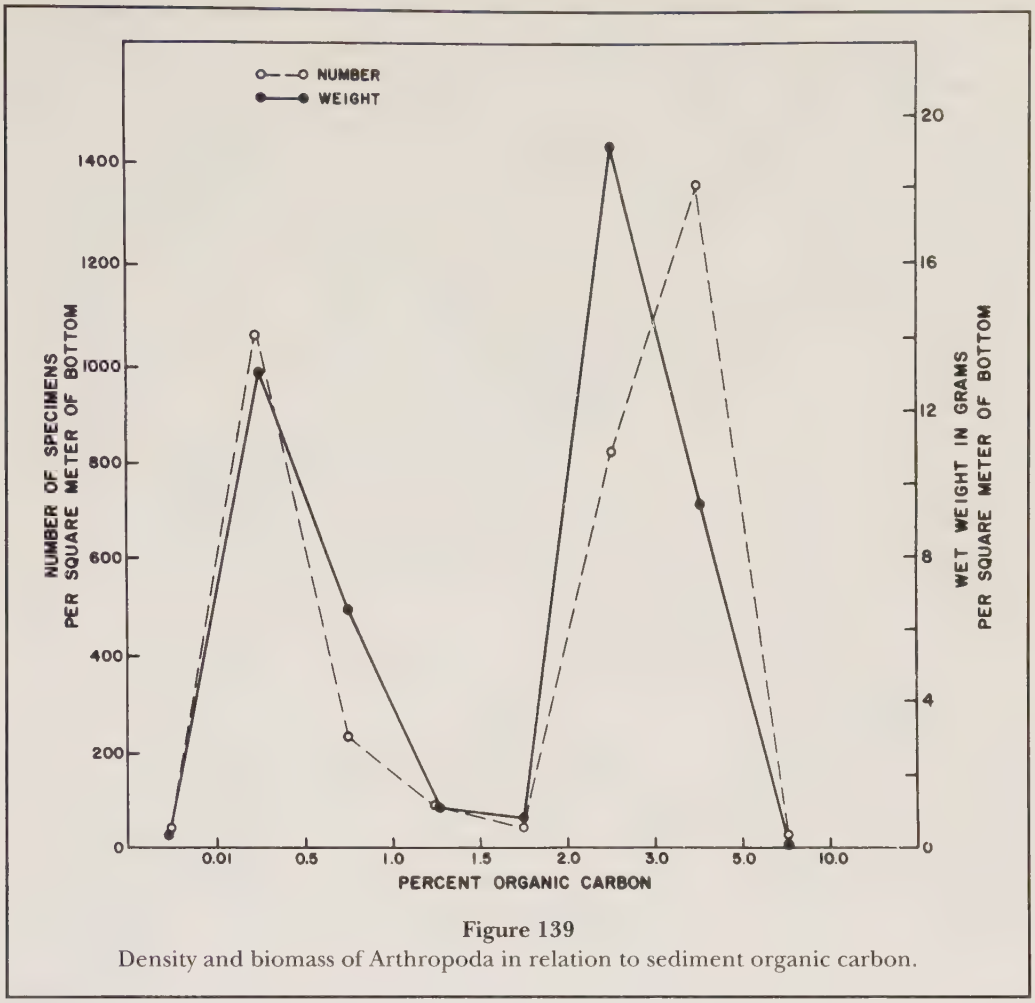


Figure 139
Density and biomass of Arthropoda in relation to sediment organic carbon.

Other studies (Wigley and McIntyre, 1964) revealed that ostracods, including specimens as small as 75 microns or less, are not abundant in the offshore Southern New England region. Their average density there was only slightly more than 1 individual/m^2.

Ostracods were taken at only five stations (0.5% of total) situated in diverse localities, all in offshore waters (Fig. 147). Two of the stations were situated on the Nova Scotia shelf, and one station was situated at each of the following locations: the Gulf of Maine, the continental slope south of Georges Bank, and the continental rise east of New Jersey. Density of these ostracods averaged <0.1/m^2 and their biomass <0.01 g/m^2 (Table 5).

Water depths at which ostracods were found ranged from 61 to 2,682 m. Their average density was slightly higher at depths below 200 m than on the continental shelf (Tables 11, 13).

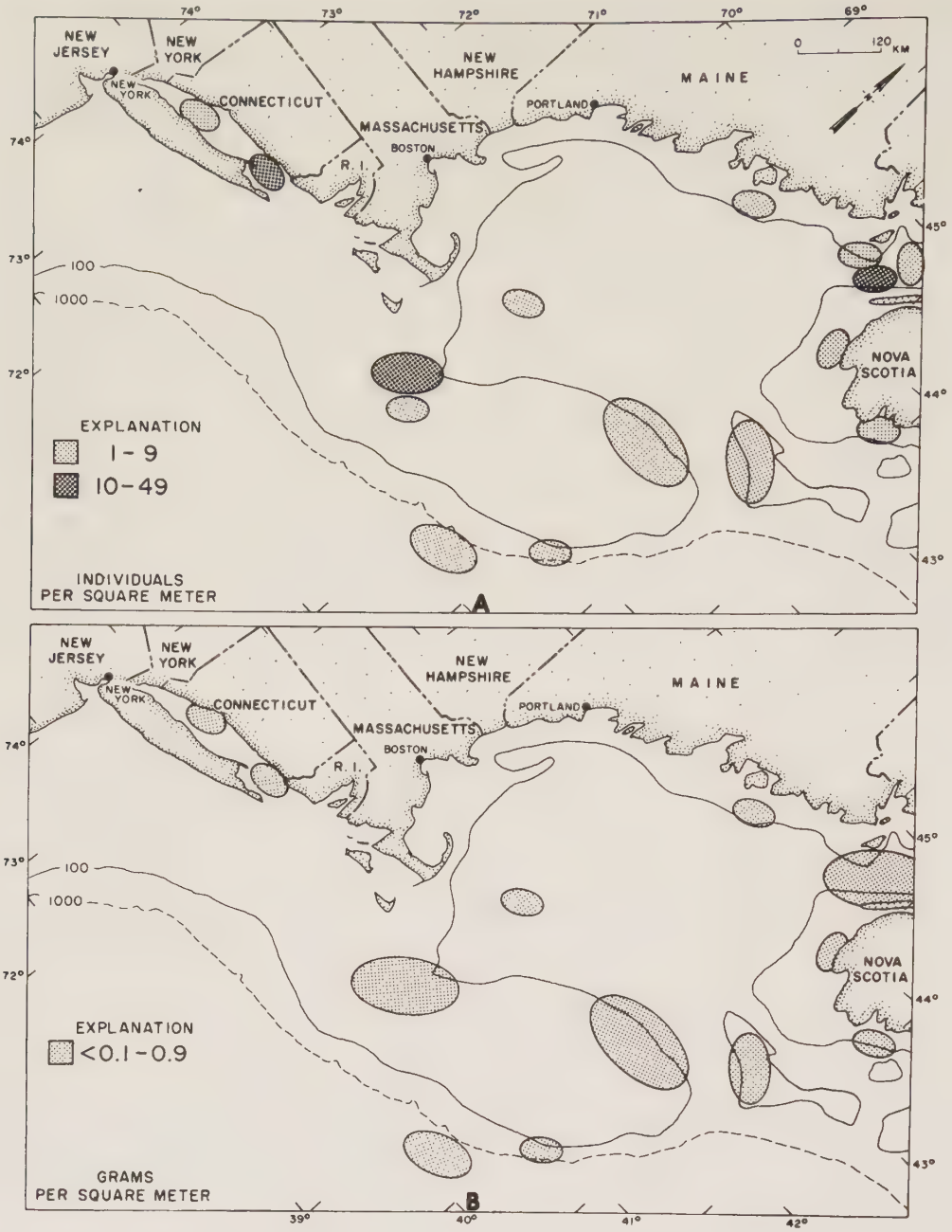
Ostracods occurred in three types of bottom sediments: gravel, sand-silt, and silt-clay. Their density was about equal in each type (Tables 16, 18).

Members of this group were found only in areas where the temperature range was below 8°C. Although their density in all areas was low, it was slightly higher where the temperature range was less than 4°C than in areas where slightly higher (4–7.9°C) ranges prevailed (Tables 21, 23).

Ostracods occurred where sediment organic carbon content levels ranged between 0.01 and 0.99%. Densities were somewhat greater at the higher levels than at the lower ones (Tables 26, 28).

Cirripedia—Barnacles were generally sparse and, except in a few local areas, made up a small proportion of the total benthic fauna. In some favorable habitats, such as rocky areas in shallow coastal waters and on offshore banks subjected to relatively strong water currents, barnacles were common to very abundant (Table 3). Densities of nearly 8,000 individuals/m^2 and biomasses of over 1,000 g/m^2 were encountered.

Members from two suborders, Balanomorpha (rock barnacles) and Lepadomorpha (stalked barnacles), were



PYCNOGONIDA

Figure 140

Geographic distribution of Pycnogonida: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

present in the collections, but those from the latter group were uncommon. The genus *Balanus* was overwhelmingly the dominant form, of which three species were common.

Rock barnacles were usually 0.5 to 1.5 cm in height and diameter; however, some newly settled specimens as small as 1 mm and a few specimens greater than 5 cm in length and diameter were collected. Stalked barnacles had a more restricted size range; they averaged 0.5 cm in length, with extremes of about 0.25 to 1 cm.

Rock barnacles were most commonly found attached to rocks, mollusk shells, and shells of other barnacles. A

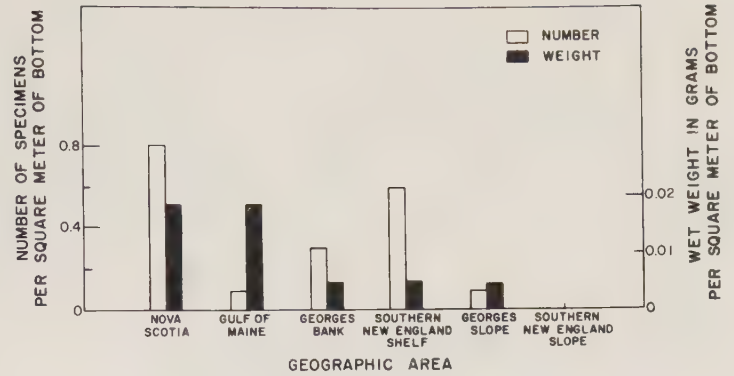


Figure 141
Density and biomass of Pycnogonida in each of the six geographic areas.

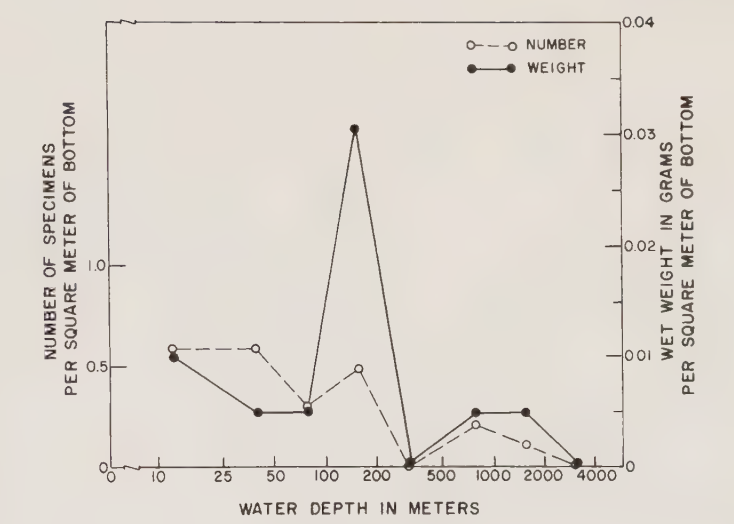


Figure 142
Density and biomass of Pycnogonida in relation to water depth.

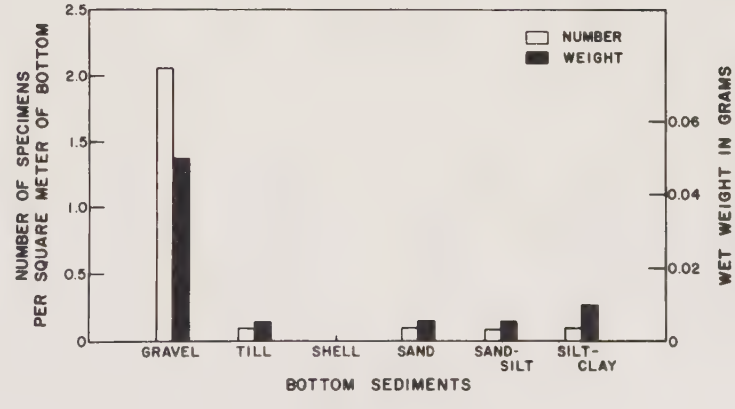


Figure 143
Density and biomass of Pycnogonida in relation to bottom sediments.

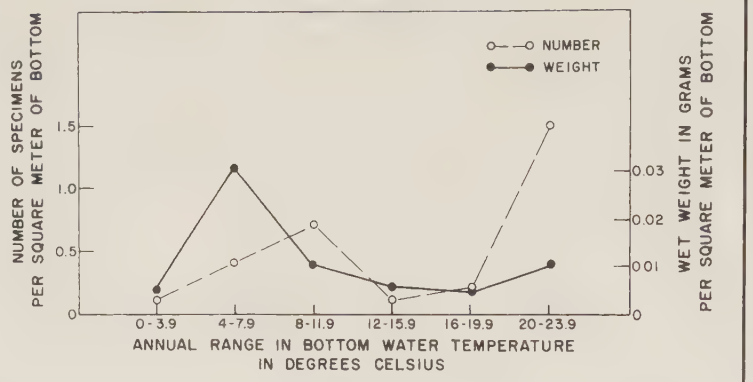


Figure 144
Density and biomass of Pycnogonida in relation to the annual range of bottom water temperature.

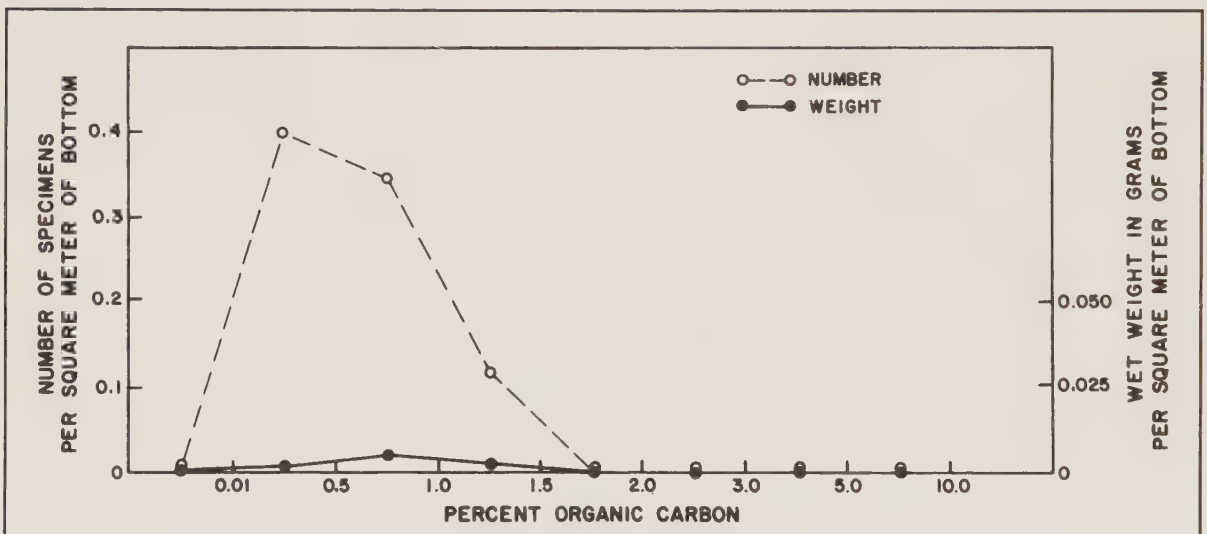


Figure 145
Density and biomass of Pycnogonida in relation to sediment organic carbon.

small proportion occurred on stalks of ascidians, on carapaces of decapod crustaceans, and on a variety of other hard to moderately hard objects. Stalked barnacles were attached to similar substrates but were relatively more common on crustaceans, hydroids, and corals.

The majority of specimens were chalky white. Rock barnacles from inshore localities sometimes had a film of yellowish or greenish algae covering their plates, and in some ridged species a brownish layer occurred in the grooves of the shell. Very large specimens were commonly light yellow and white, whereas some of the very small ones were pale gray. Stalked barnacles generally had white shells on both the capitulum and peduncle, but a few specimens had delicate shades of rose on the larger plates. The color of the peduncle ranged from yellow to grayish brown.

Cirripedia occurred in 41 samples (4% of total). Their density averaged 21.8/m^2. Their biomass averaged 3.39 g/m^2 (Table 5).

Geographic Distribution

Barnacles were found at scattered locations along the entire length of the region's continental shelf (Fig. 148). Coastal regions, shoals, and banks were the most

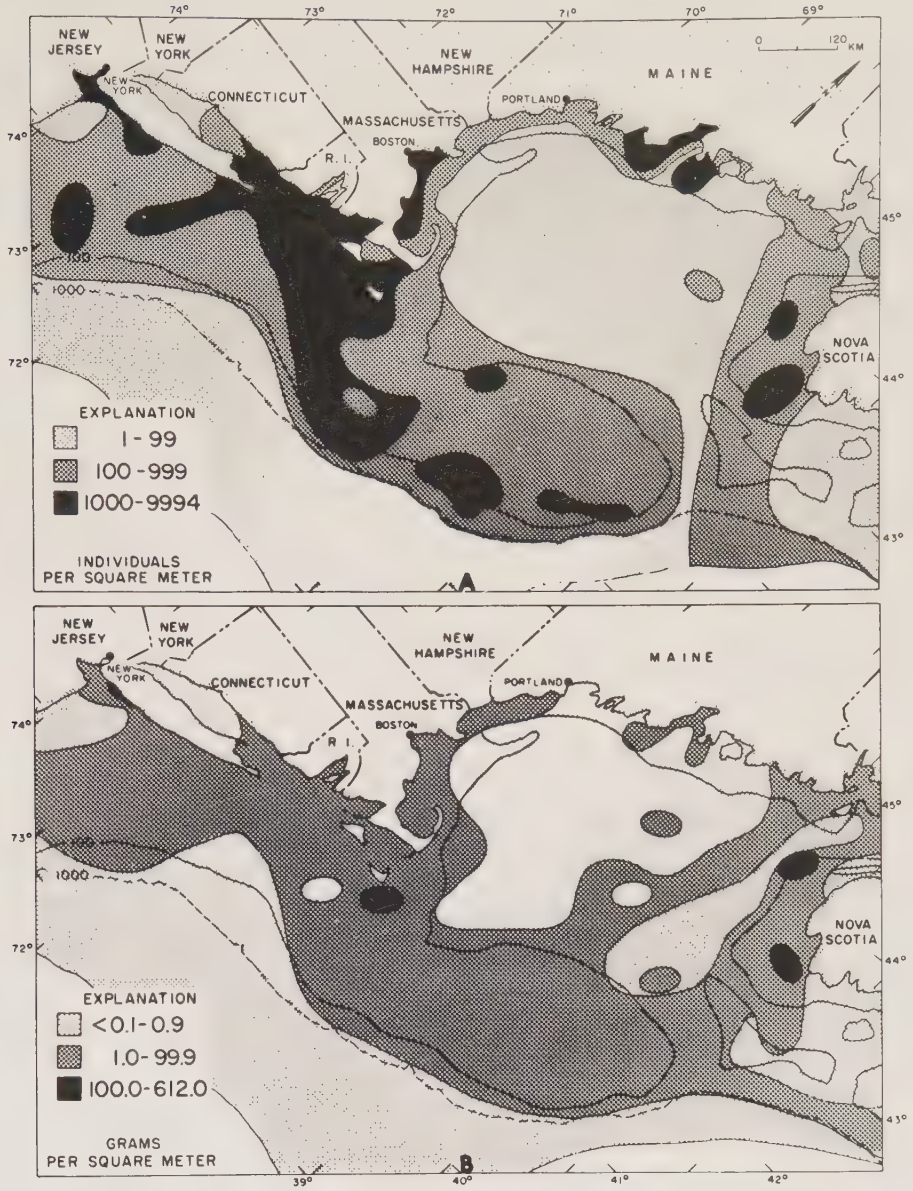
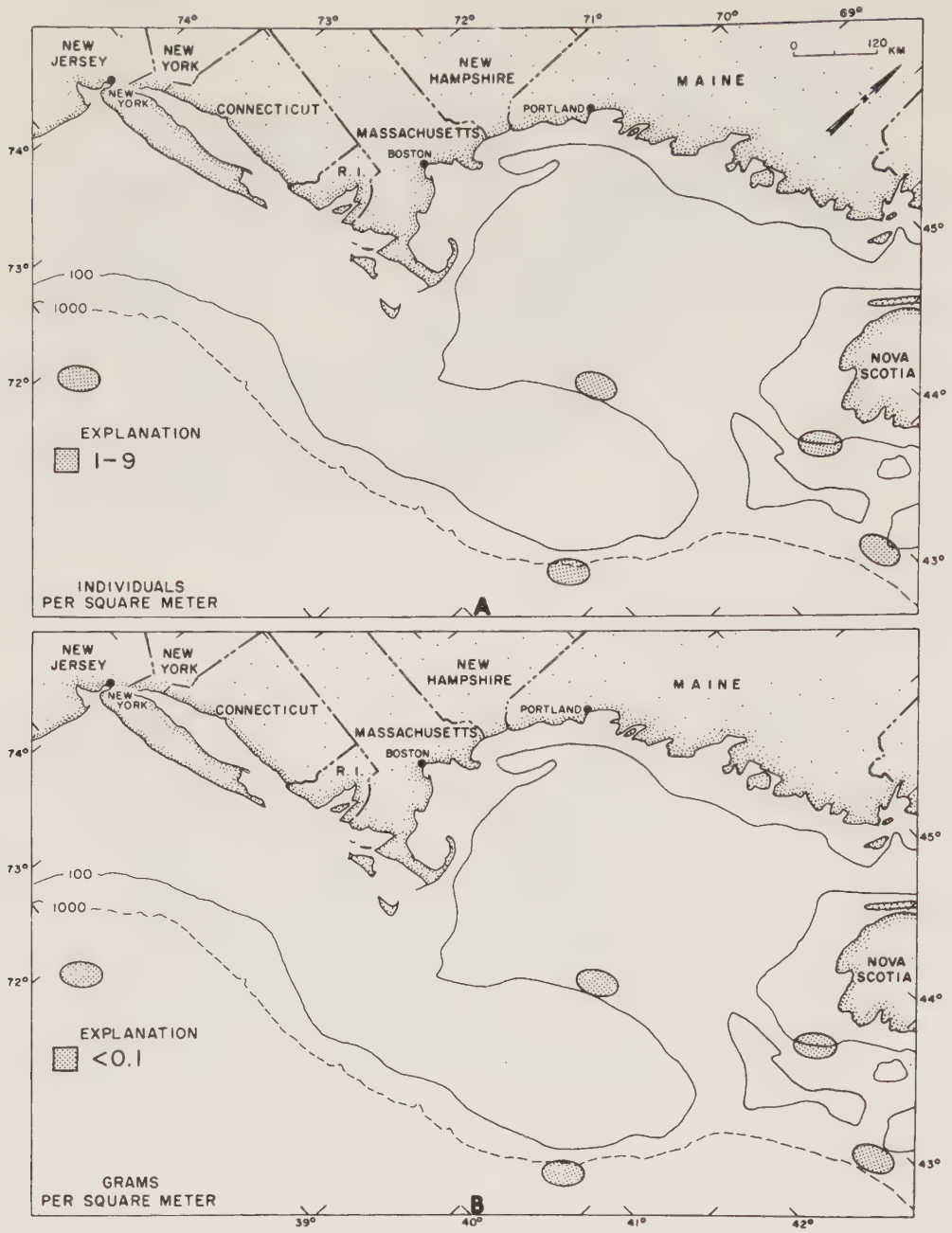


Figure 146
Geographic distribution of Crustacea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

commonly inhabited areas. They were absent from almost all of the continental slope and from much of the central Gulf of Maine. Densities of from 1 to 49 individuals/m^2 and biomasses of less than 10 g/m^2 were most prevalent, but large quantities (100–5,000 individuals and 50–612 g/m^2) were not unusual in the coastal and nearshore localities.

Barnacles were present in four of the six standard geographic areas; they were absent from Georges Slope and the Southern New England Slope (Table 6; Fig. 149). The two areas where they were especially abundant were the Southern New England Shelf (52/m^2) and Nova Scotia (36/m^2). Densities in the Gulf of Maine and on Georges Bank were only 3 and 6/m^2, respectively.

Biomass in Nova Scotia was larger (13 g/m^2) than on the Southern New England Shelf (7 g/m^2) even though densities were higher in the latter area (Table 8; Fig.



OSTRACODA

Figure 147

Geographic distribution of Ostracoda: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

149). Thus the average size of individual barnacles was larger (0.36 g) in Nova Scotia than on the Southern New England Shelf (0.13 g). The biomass of barnacles in the Gulf of Maine and on Georges Bank was less than 0.5 g/m^2.

Frequency of occurrence was highest (15% of the samples) in the Nova Scotia area and substantially lower (2 to 4%) in the remaining shelf areas. They were absent in the two slope areas (Table 10).

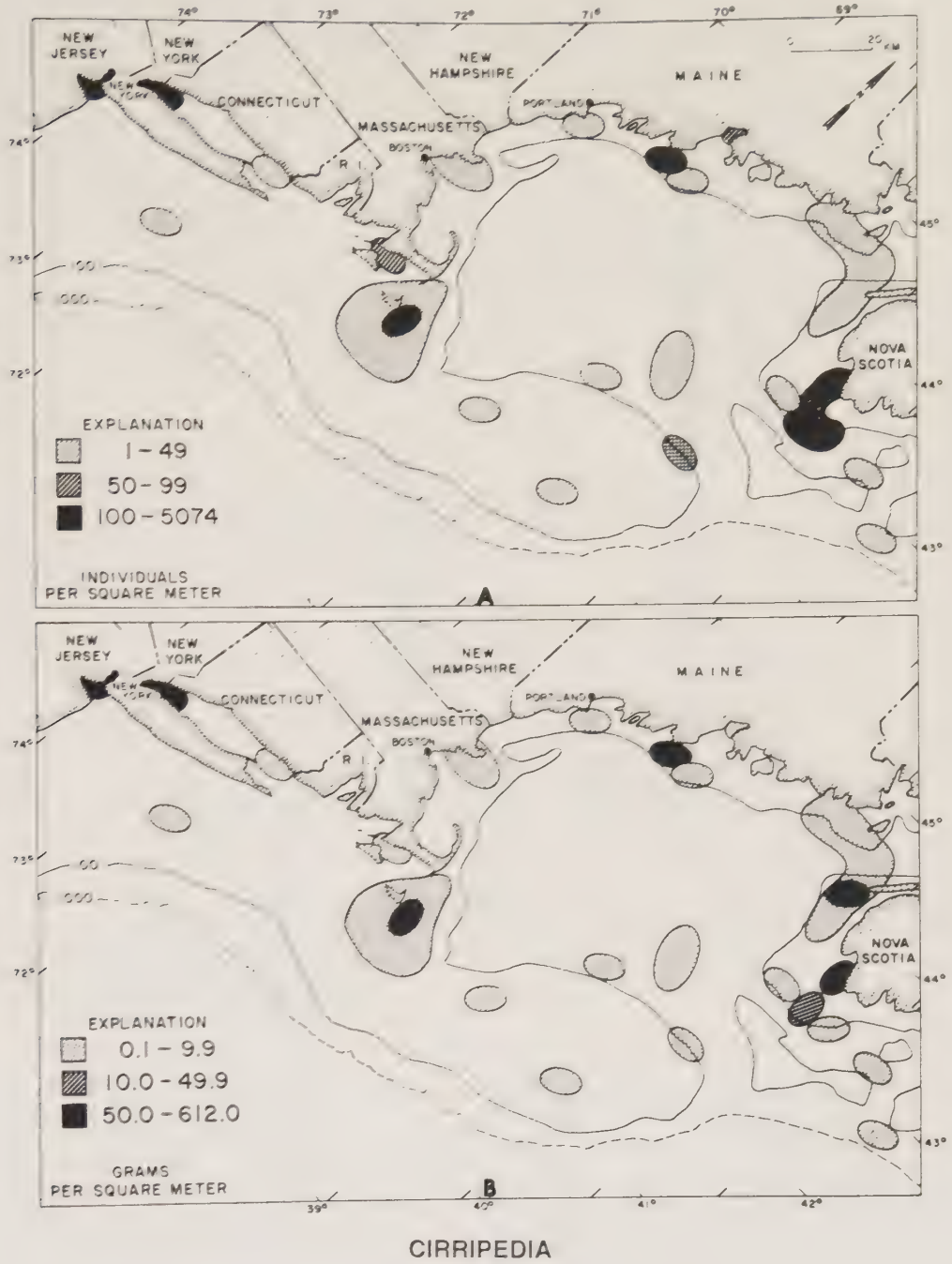


Figure 148

Geographic distribution of Cirripedia: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

Bathymetric Distribution

Barnacles were limited to the rather shallow depth range of 8 to 329 m. They were substantially more plentiful (214 individuals/m^2) in shallow water and diminished sharply in abundance with increasing water depth (Table 11; Fig. 150). Densities on the outer continental shelf and upper slope were 2.3 and 0.7 individuals/m^2, respectively.

Biomass of barnacles in relation to bathymetric distribution was similar to that of numerical density. Biomass was largest (27 g/m^2) in shallow water and de-

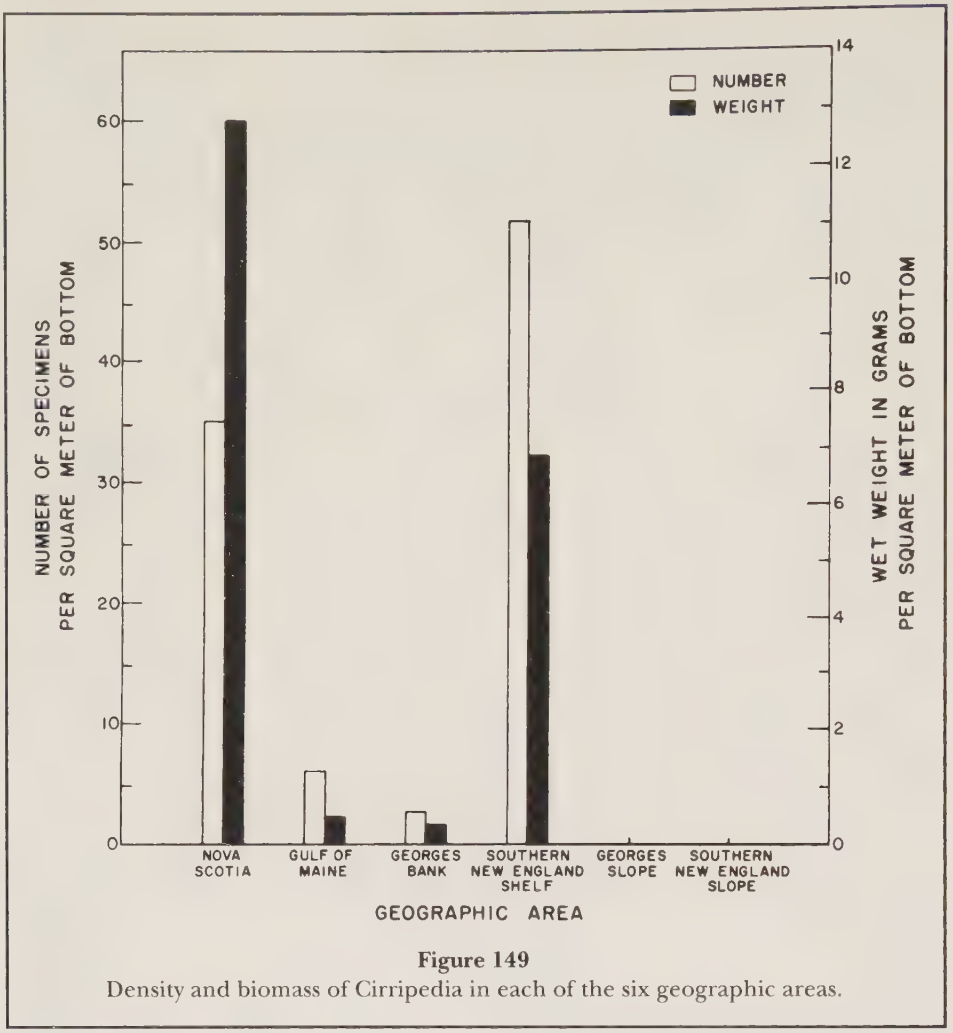


Figure 149
Density and biomass of Cirripedia in each of the six geographic areas.

creased with increasing depth (to 0.1 g/m^2 at 100–199 m) (Table 13; Fig. 150). An exception to this trend occurred in the 200–499 m depth class. In this deepwater zone the density was low but the biomass was much larger (2.5 gm^2) than the general trend would have indicated. This relatively large value may have been due to the presence of *Balanus hameri* in this depth class. This species is exceptionally large and occurs in moderately deep water.

Barnacles occurred in only a small proportion of the samples, but they were much more common (13%) in the shallow depth class (0–24 m) than in the other classes (3 to 4%). None were present in depths greater than 500 m (Table 15).

Relation to Sediments

Barnacles were found in all sediment types of the New England region that were sampled. Their average density was, surprisingly, highest (56 individuals/m^2) in sand-silt sediments (Table 16; Fig. 151). Moderate densities (29 and 16 individuals/m^2) occurred on gravel and sand bottoms. The other sediment types yielded low (<5/m^2) densities.

The biomass of barnacles was largest (11 g/m^2) on gravel bottoms and was moderate (4.4 and 2.4 g/m^2) in sand-silt and sand. Low quantities (<0.5 g/m^2) prevailed in the other sediments (Table 18; Fig. 151).

The unexpectedly high density of cirripedes in sand-silt bottoms resulted from high concentrations of small specimens (average weight <0.1 g) in a small proportion (3%) of the samples. Small barnacles densely colonize occasional mollusk shells and other firm substrates, often of biogenic origin, but rarely are they able to attain large size in these habitats. Conversely, on gravel bottoms the average size of individual barnacles was 0.3 to 0.4 g.

Frequency of occurrence of barnacles was low in all types of bottom sediments. Shell and gravel ranked

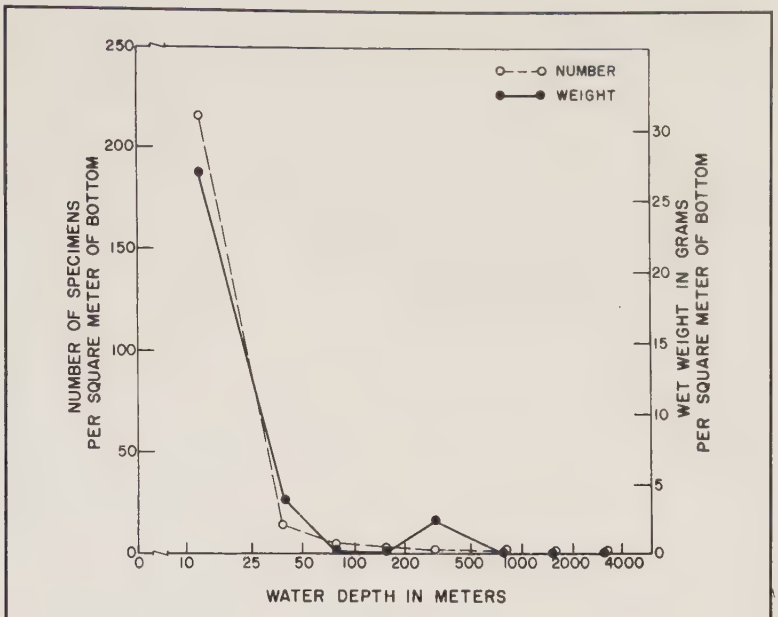


Figure 150
Density and biomass of Cirripedia in relation to water depth.

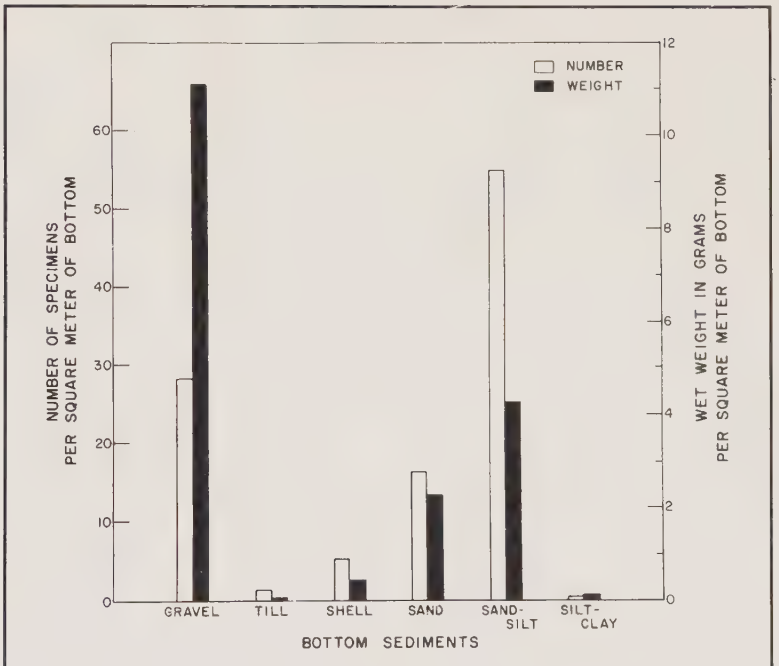


Figure 151
Density and biomass of Cirripedia in relation to bottom sediments.

highest with an incidence rate of 13 to 17%. The rate was moderately high in till, but in all other types they were present in less than 3% of the samples (Table 20).

Relation to Water Temperature

Barnacles occurred throughout the entire temperature range spectrum of the New England region (Table 21; Fig. 152). There was a pronounced increase in density as

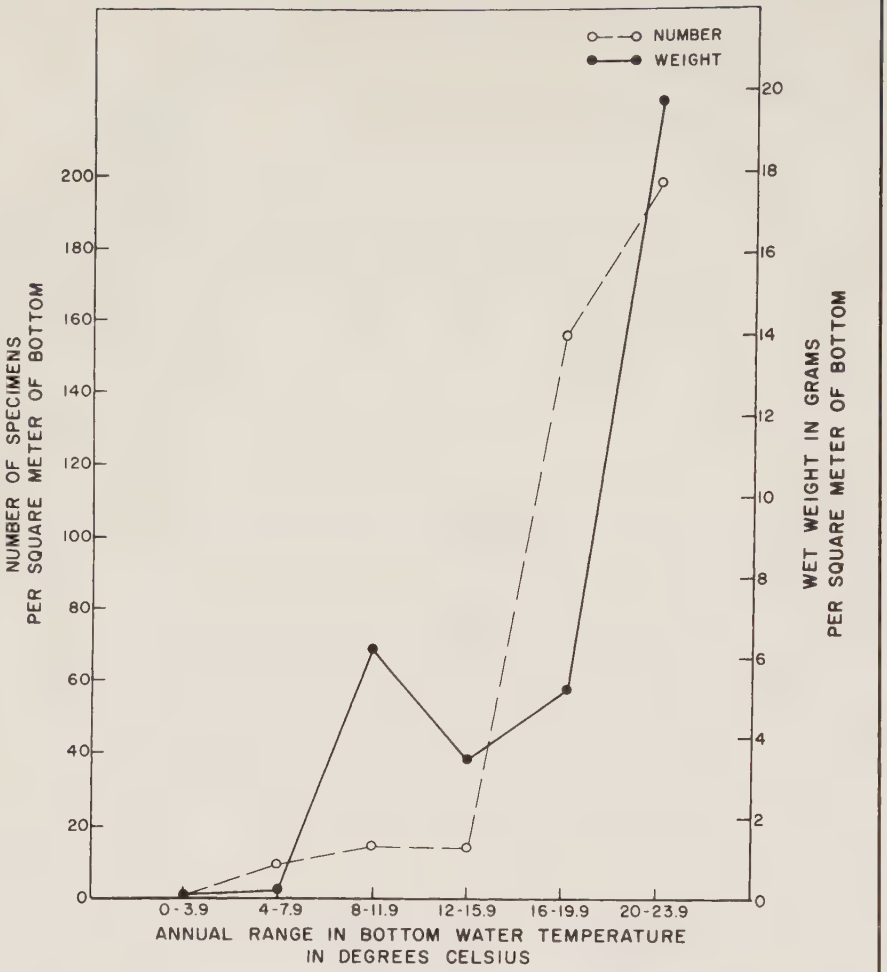


Figure 152
Density and biomass of Cirripedia in relation to the annual range of bottom water temperature.

the temperature range broadened. This trend was very pronounced. Their density was 0.3/m^2 where the temperature range was nil or small. Their density steadily increased to 196/m^2 where the temperature range was greatest.

Biomass similarly showed a marked increase in relation to increased temperature range. The range in average biomass was from 0.05 to 20.32 g/m^2, the extreme values occurring in the two extreme temperature range classes (Table 23; Fig. 152).

Frequency of occurrence of cirripedes was rather low (2 to 5% of the samples) in all temperature range classes except the highest (20°–23.9°C), where a moderate (18%) incidence rate was obtained (Table 25).

Relation to Sediment Organic Carbon

There was a distinct bimodal relationship of cirripede abundance with regard to organic carbon content of the sediment. This was especially apparent in terms of density. Moderate densities (19 and 39 individuals/m^2) occurred in the two carbon content range classes between 0.01 and 0.99%; none occurred in content classes between 1.00 and 1.99%; but density increased dramatically to 613/m^2 where carbon content was from 2.00 to 2.99%, and was moderately high (83/m^2) in carbon contents between 3 and 5% (Table 26; Fig. 153).

Biomass displayed a similar trend but not as dramatically. Moderate biomass (6.5 and 4.1 g/m^2) occurred in the two range classes between 0.01 and 0.99%, with highest biomass (14.3 g/m^2) in the 2.00 to 2.99% class (Table 28; Fig. 153). Lowest biomass was in the highest organic content class.

Frequency of occurrence of barnacles was moderate (3 and 6%) in the lower level organic carbon content classes but was moderately high (15 and 25%) in the

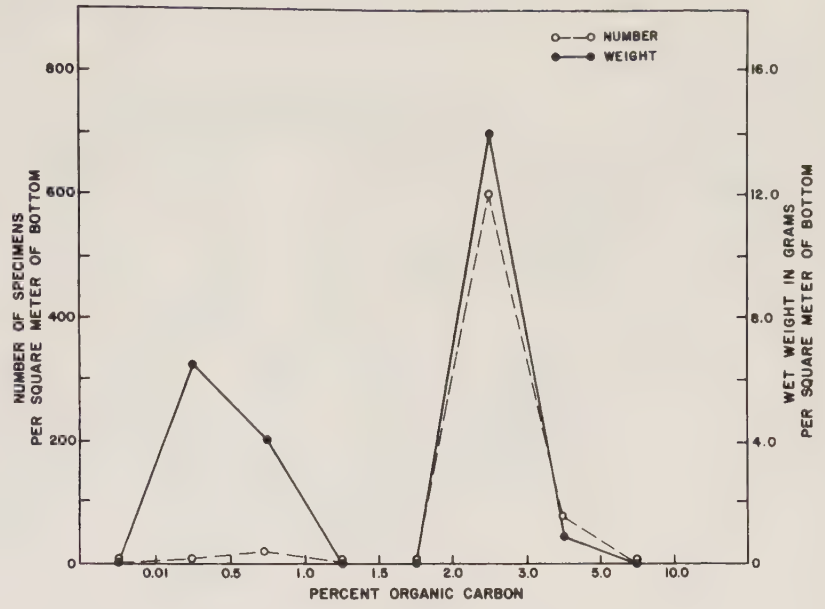


Figure 153
Density and biomass of Cirripedia in relation to sediment organic carbon.

higher level classes, reflecting the trends established by density and biomass (Table 30).

Copepoda—Only four of our samples contained specimens of Copepoda, representing only 0.4% of the total samples. The small size of members of this group in relation to the sampling methods used in this study led to incomplete sampling and the attendant extremely conservative abundance estimates.

Copepoda represented less than 0.1% of the total macrofaunal biomass and density (Table 3). A total of 26 specimens was obtained, yielding a mean density of $<0.1/m^2$ and a mean biomass of <0.01 g/m^2 (Table 5).

Samples containing copepods were located in the Southern New England Shelf and Slope subareas. Depth ranges occupied were 50–99 m, 200–499 m and 500–599 m. Copepods were present in three sediment types (sand, sand-silt, and silt-clay), in two temperature range classes (0–3.9° and 12–15.9°C), and in the three organic carbon content classes between 0.01 and 1.49%.

Values of copepod biomass and density for each environmental parameter considered in this report may be found in Tables 6–30.

Cumacea—Cumaceans are marine peracarid crustaceans that were widely distributed and well represented in New England waters (Theroux and Schmidt-Gengenbach[7]). Twenty-three species in 13 genera belonging to 5 families were identified in our samples from the New England region. Cumaceans were among the subdominant taxa in terms of density, providing 1.7% of the total number of specimens, but owing to their small size, were much less important in terms of biomass, contributing only 0.1% of the total (Table 3).

Cumaceans in our collections ranged from 7 to 15 mm in length; most were between 8 and 12 mm long.

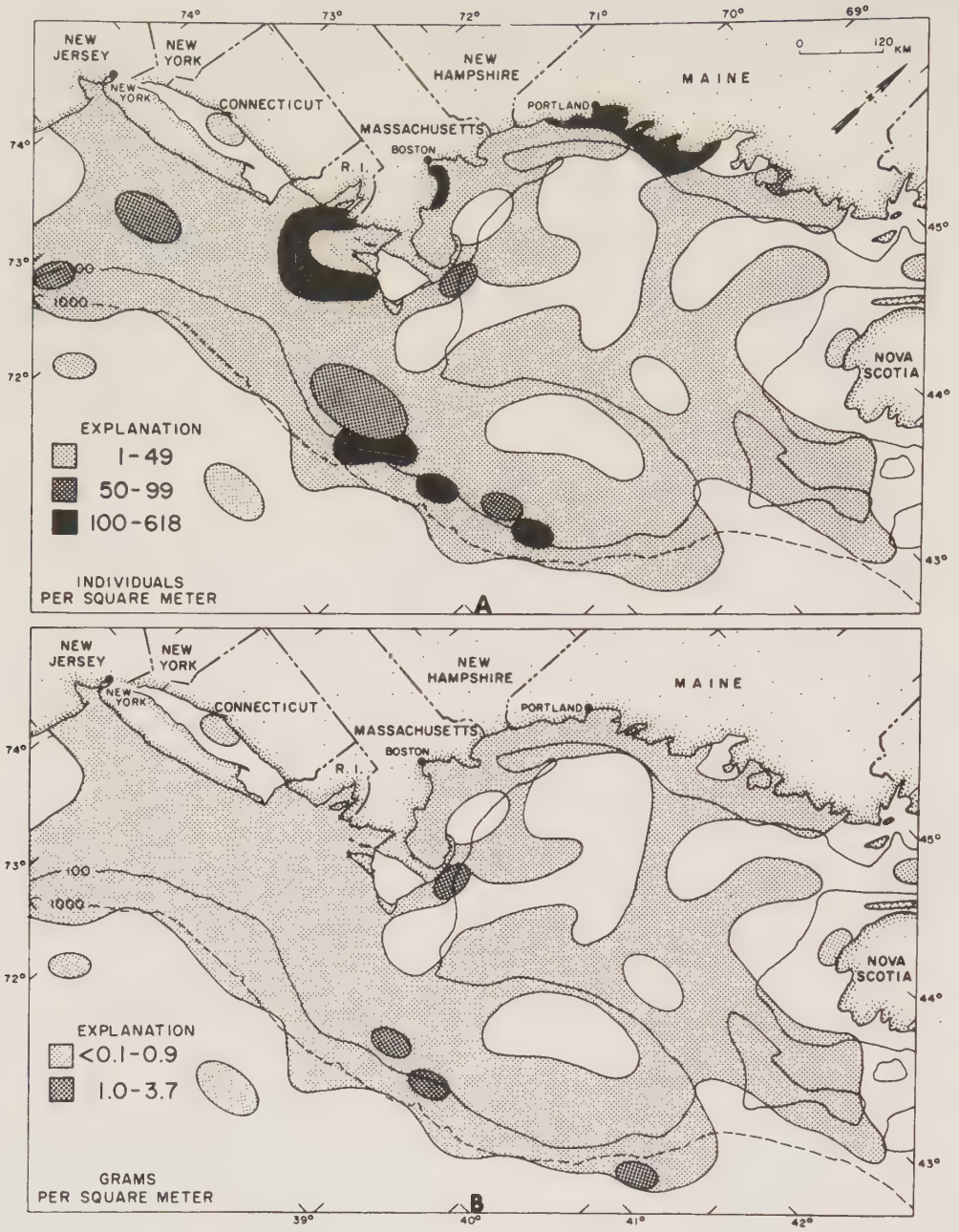
Color of our specimens was mostly drab olive to olive brown with a few lighter in color and mottled by dark spots.

The majority of cumaceans are bottom dwellers that were found buried in sand and mud, filter feeding or browsing organic matter from sand grains. Many exhibit diel excursion to the surface or into the water column where they swarm at night.

Cumaceans occurred in 390 samples (36% of the total), yielding a total of more than 27,500 specimens (Table 5). Their mean density was 26/m^2, and mean biomass was 0.11 g/m^2.

Geographic Distribution

Although found throughout the study area, cumaceans showed some interesting patterns of absence, especially in the Gulf of Maine. These distributional patterns reflect the rather restricted sediment particle size preferences of cumaceans. They tend to favor sediments of medium to medium-fine particle sizes that are most prevalent in the sand fractions, and shun the coarser (gravels, tills, shelly fractions) and finer (sandy silts, silts and clays) fractions. The Nova Scotian shelf and Gulf of Maine each contain extensive deep basins floored with fine muds, as well as shallower banks paved with



CUMACEA

Figure 154

Geographic distribution of Cumacea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

cobbles, gravels, and coarse sands; the central part of Georges Bank is largely made up of coarse shifting sands; and Nantucket, Vineyard, and Long Island Sounds contain large expanses of very fine muds and silts. Most of these areas were devoid of cumaceans (Fig. 154).

Average densities ranged from 1 to 618 individuals/m^2. The majority of the region contained moderate densities (1–49/m^2) with medium size patches of intermediate (50–99/m^2) density at continental shelf depths, and high (100–618/m^2) density along the southern edge of Georges Bank and along the coasts of Maine, Massachusetts, and Rhode Island.

Average biomass was low (<0.1–0.9 g/m^2) over most of their range with only small patches of moderately

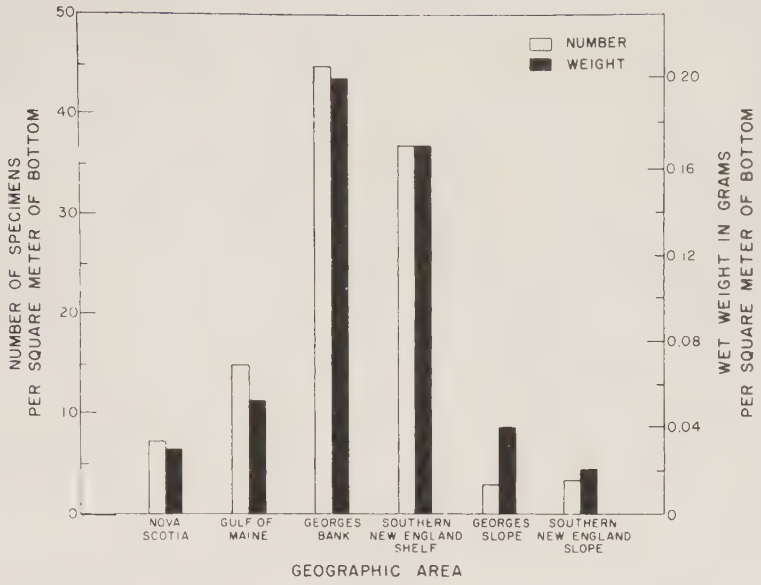


Figure 155
Density and biomass of Cumacea in each of the six geographic areas.

low biomass (1–4 g/m^2) along the shelf break on Georges Bank and the eastern shore of Cape Cod.

Among the standard geographic areas, Georges Bank and the Southern New England Shelf yielded the highest mean densities (45 and 37/m^2, respectively) and biomass (0.20 and 0.17 g/m^2, respectively).

Lower densities and biomasses occurred in the Gulf of Maine and Nova Scotia shelf, and lowest values for both measures occurred in the two slope areas (Tables 6, 8; Fig. 155).

Frequency of occurrence was moderately high in all geographic areas with from 19 to 49% of the samples containing specimens of cumaceans (Table 10).

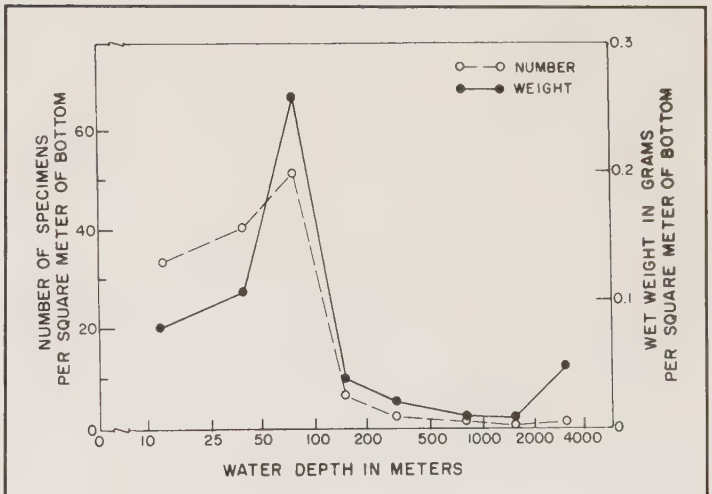


Figure 156
Density and biomass of Cumacea in relation to water depth.

Bathymetric Distribution

Cumaceans were obtained at depths from 4 to 2,840 m. They were most plentiful, however, at depths shallower than 100 m. The three depth zones between 0 and 100 m contained significantly higher mean densities than the deeper zones, ranging from 50 to 33/m^2 as depth decreased, whereas in the deeper (≥100 m) ones they ranged from 7 to 0.7/m^2 as depth increased to 1,999 m. In the deepest zone (2,00–3,999 m) mean density was 2/m^2 (Table 11; Fig. 156).

The trend for biomass in relation to depth was similar to that for density but was from one to three orders of magnitude lower. Mean biomass ranged from 0.26 to 0.08 g/m^2 in waters 100 m and less in depth and was lower still at deeper (>100–1,999 m) sites, ranging from 0.04 to 0.01 g/m^2 with increasing depth. The deepest zone contained a mean biomass of 0.05 g/m^2 (Table 13; Fig. 156).

Cumaceans were well represented in the samples in each depth class. Four depth classes, the three between 25 and 200 m and the 500–999 m class, each yielded specimens in over 30% of the samples (range: 30–

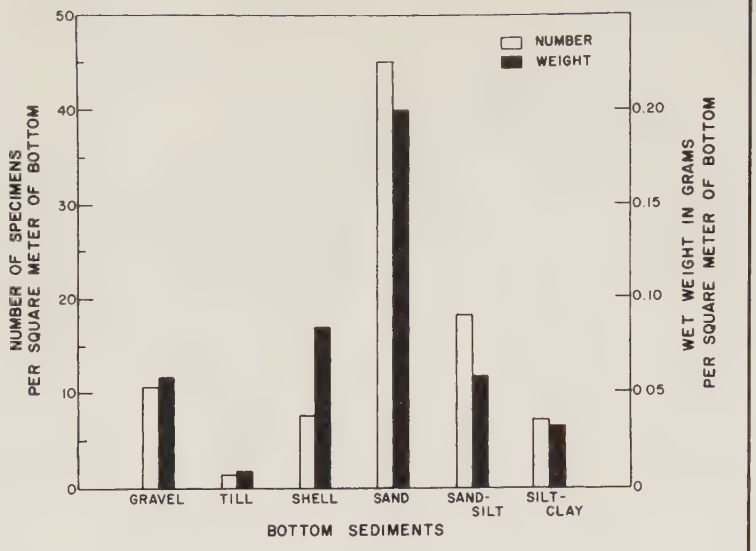


Figure 157
Density and biomass of Cumacea in relation to bottom sediments.

56%), while the other depth classes had frequencies over 15% (Table 15).

Relation to Sediments

Cumaceans occurred in all sediments found in the region but in significantly different proportions. Sand, sand-silt, and gravel contained the greatest numbers of individuals, with mean densities of 45, 18, and 11/m^2, respectively; shell and silt-clay sediments yielded moderate mean densities (8 and 7/m^2, respectively), with smallest (1/m^2) amounts in till substrates (Table 16; Fig. 157).

The trend for biomass was essentially similar to that of density but at much reduced levels (Table 18; Fig. 157). Sand, shell, and sand-silt contained mean biomasses of 0.20, 0.08, and 0.06 g/m^2, respectively, while the values for gravel, till, and silt-clay were 0.06, 0.01, and 0.03 g/m^2, respectively.

The frequency of occurrence of cumaceans ranged from 50 to 26%, in samples from sand, sand-silt, and gravel and was between 14 and 22% in the other sediment types (Table 20).

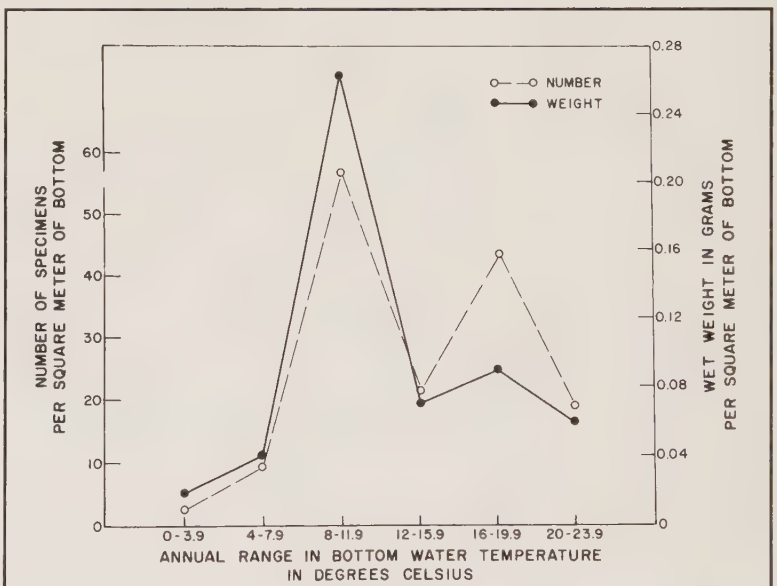


Figure 158
Density and biomass of Cumacea in relation to the annual range of bottom water temperature.

Relation to Water Temperature

Both measures of cumacean abundance showed a bimodal trend in relation to annual range in bottom water temperature. The greatest numerical abundance (56/m^2) and biomass (0.26 g/m^2) occurred where temperature range was moderate (8–11.9°C), followed by another peak in areas experiencing a somewhat higher (16–19.9°C) range where high density (44/m^2) but considerably lower (0.09 g/m^2) biomass occurred (Tables 21, 23; Fig. 158). Density was also relatively high in the two other high temperature range classes (12–15.9° and >20°C) but fell off considerably in the more stable temperature regimes with ranges between

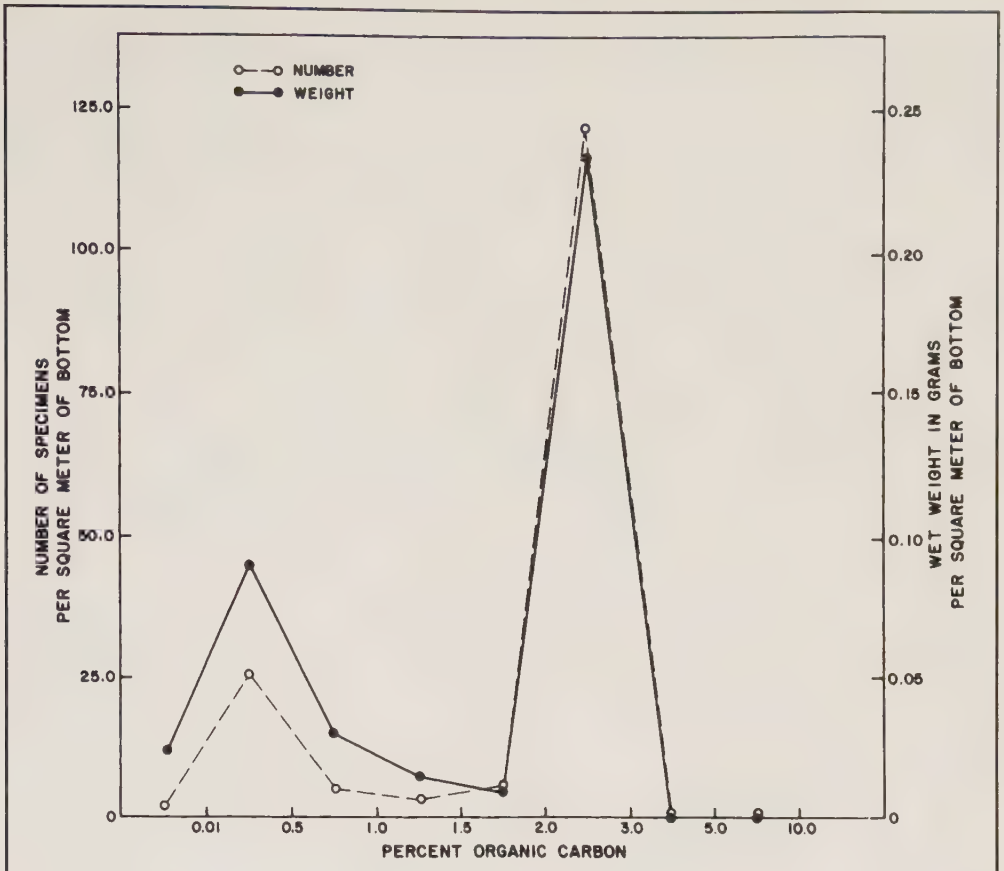


Figure 159
Density and biomass of Cumacea in relation to sediment organic carbon.

0 and 7.9°C. Biomass values, although at a much lower level, were similarly affected.

Frequency of occurrence of cumaceans in samples in the various temperature range classes was fairly equal (ranging from 31 to 38%) in all but two: the 8–11.9°C class had a 54% occurrence and the 0–3.9°C class had a 19% rate (Table 25).

Relation to Sediment Organic Carbon

Among the various taxa considered in this study, Cumacea is one of only a few which showed a marked preference in relation to organic carbon content. Sediments containing 2.00–2.99% organic carbon were clearly preferred over all other content classes (Tables 26, 28; Fig. 159). There the mean density of cumaceans was 123/m^2 with a mean biomass of 0.24 g/m^2, reflecting, no doubt, the habit adopted by many species of browsing organic matter from sand grains. Another peak in abundance (25/m^2 and 0.09 g/m^2) occurred in the much lower organic carbon content class 0.01–0.49% Significantly lower densities and biomasses occurred in the other carbon content classes, and none occurred in levels above 3%.

The highest frequency of occurrence, 44%, was in the 0.01–0.49% content class followed by the 2.00–2.99% class, in which 31% of the samples yielded specimens of cumaceans. Twelve to 29% of the samples in the other content classes in which they occurred provided specimens (Table 30).

Tanaidacea—Tanaidaceans are peracaridan crustaceans generally considered to be transitory forms between the Mysidacea-Cumacea and the Isopoda. The order is made up of four families, but only two, the Paratanaidae and Neotanaidae, were represented in our collections.

Although our specimens were collected in relatively deep water, tanaidaceans can be found from between tide marks to ultra-abyssal depths exceeding 9,000 m. They inhabit burrows, tubes, or rock crevices. Some species are known to inhabit sponges; others may be found on algae or the shells of bivalve mollusks, barnacles, and other animal groups.

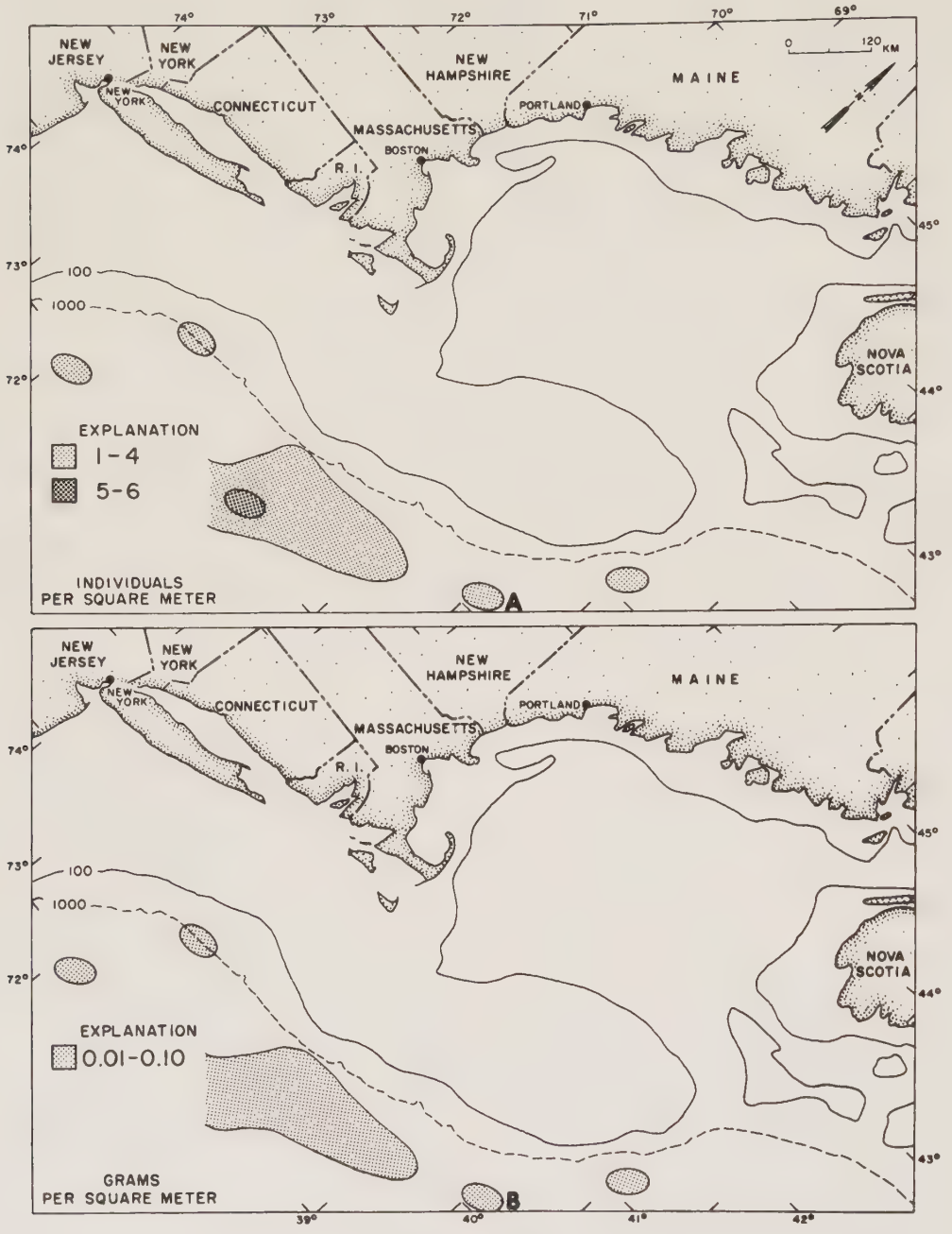
Tanaidaceans attain lengths of 2 cm or more, but most specimens in our samples were generally small in size, usually less than 0.5 cm long.

The color of our specimens was most commonly whitish and tinged with light green or light tan. Some specimens bore small brownish patches in the head region.

Tanaidaceans occurred in 15 samples (1% of total). Their density averaged <0.1/m^2 and their biomass averaged <0.01 g/m^2 (Table 5).

Geographic Distribution

Tanaidaceans were present only on the continental slope and continental rise south of Georges Bank and Southern New England (Fig. 160). They occurred in low density (6 individuals or less/m^2), and their biomass was very small (<0.01 to 0.10 g/m^2) in all sectors.



TANAIDACEA

Figure 160

Geographic distribution of Tanaidacea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

None were present in quantitative samples from the continental shelf even though previous studies and our own nonquantitative samples have revealed their presence in certain habitats in the intertidal and shallow sublittoral areas along the coast. They appear to be rare or absent from most of the outer continental shelf areas in the New England region.

Tanaidaceans were present in only two of the six standard geographic areas: Georges Slope and Southern New England Slope (Tables 6, 8; Fig. 161). Average density in each area was 0.4 individual/m^2 with an average biomass of 0.01 g or less/m^2.

Members of this group were present in 15% of the samples from Georges Slope and in 9% of samples from Southern New England Slope (Table 10).

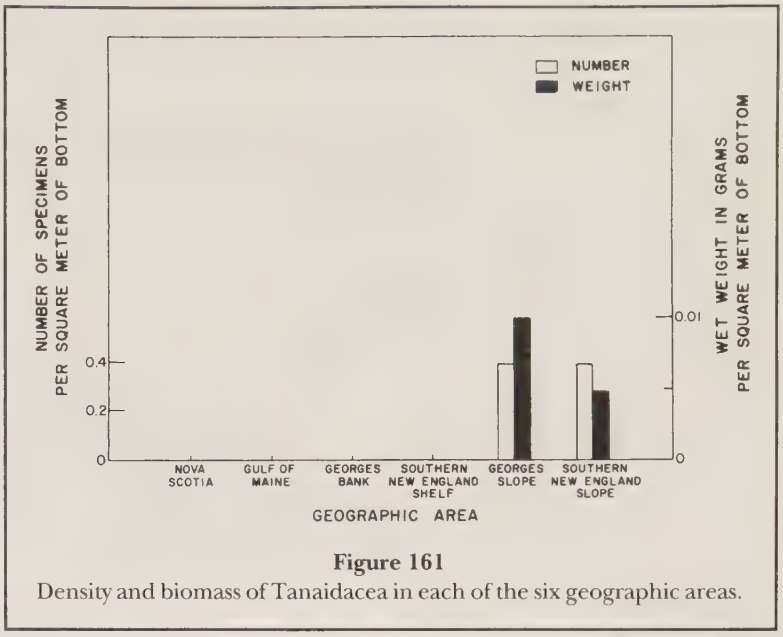


Figure 161
Density and biomass of Tanaidacea in each of the six geographic areas.

Bathymetric Distribution

In the present study tanaidaceans were found only in water depths ranging from 366 to 3,820 m (Table 11; Fig. 162). Their density was low in all depth classes within the range of their occurrence but was relatively higher (averaged 1 individual/m^2) in depths greater than 2,000 m than at shallower depths, where they averaged only 0.1 of an individual/m^2.

Biomass revealed a trend similar to that of numerical density. The biomass averaged <0.01 g/m^2 in the shallower depth classes, and 0.01 g/m^2 in deep water (Table 13; Fig. 162).

Frequency of occurrence disclosed trends similar to both density and biomass. The occurrence rate of tanaidaceans at depths greater than 2,000 m was 35%, an unusually high ratio compared to only 1 to 3% occurrence in the shallower portion of their bathymetric range (Table 15).

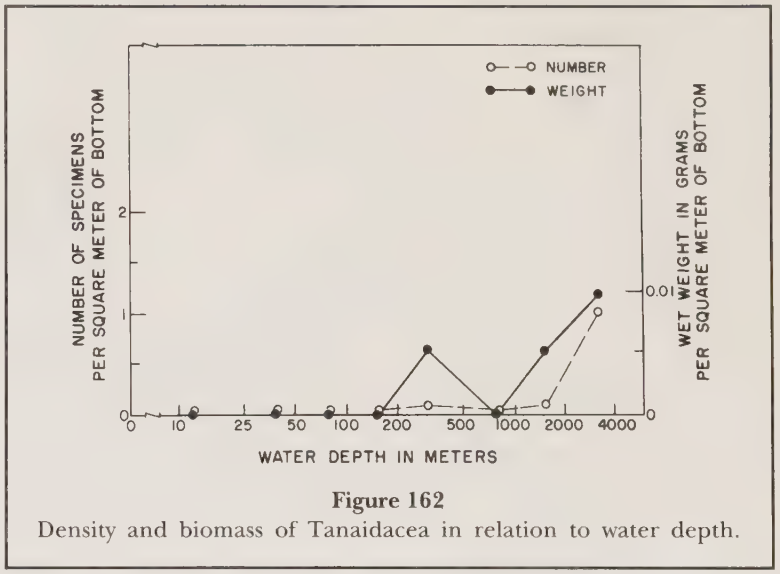


Figure 162
Density and biomass of Tanaidacea in relation to water depth.

Relation to Sediments

Tanaidaceans were found only in soft, fine-grain sediments: sand-silt and silt-clay (Tables 16, 18, 20; Fig. 163). Density, biomass, and frequency of occurrence were very low and approximately equal in both sediment types.

Relation to Water Temperature

Tanaidaceans were encountered only in areas where the annual temperature range was less than 8°C (Tables 21, 23, 25; Fig. 164). All of the measures of abundance (density, biomass, and frequency of occurrence) were very low in each of the two temperature range classes (0°–3.9° and 4°–7.9°C) in which tanaidaceans occurred.

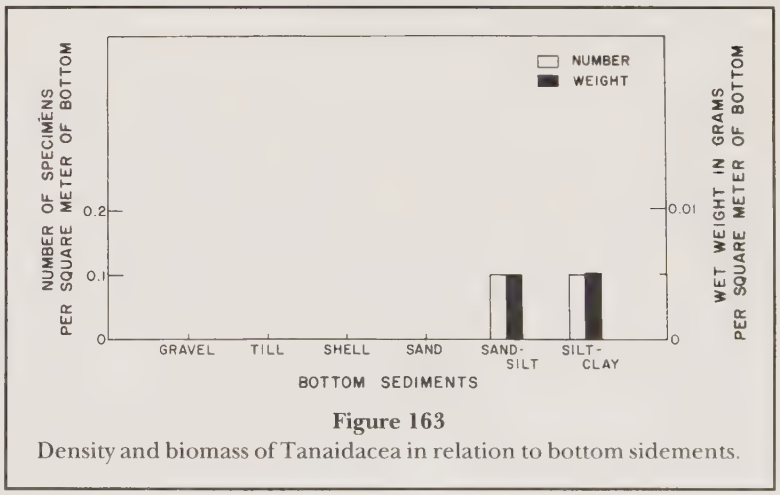


Figure 163
Density and biomass of Tanaidacea in relation to bottom sidements.

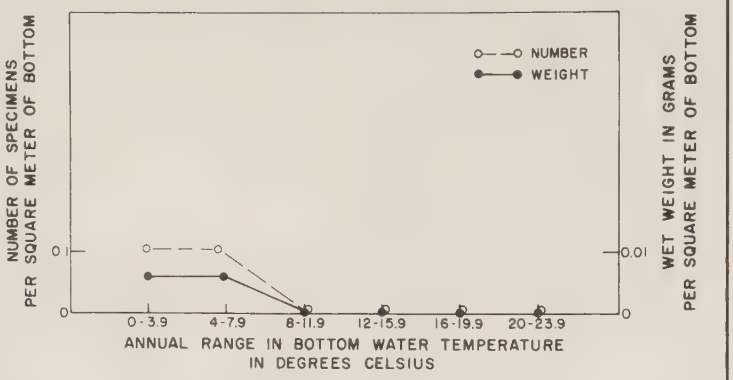


Figure 164
Density and biomass of Tanaidacea in relation to the annual range of bottom water temperature.

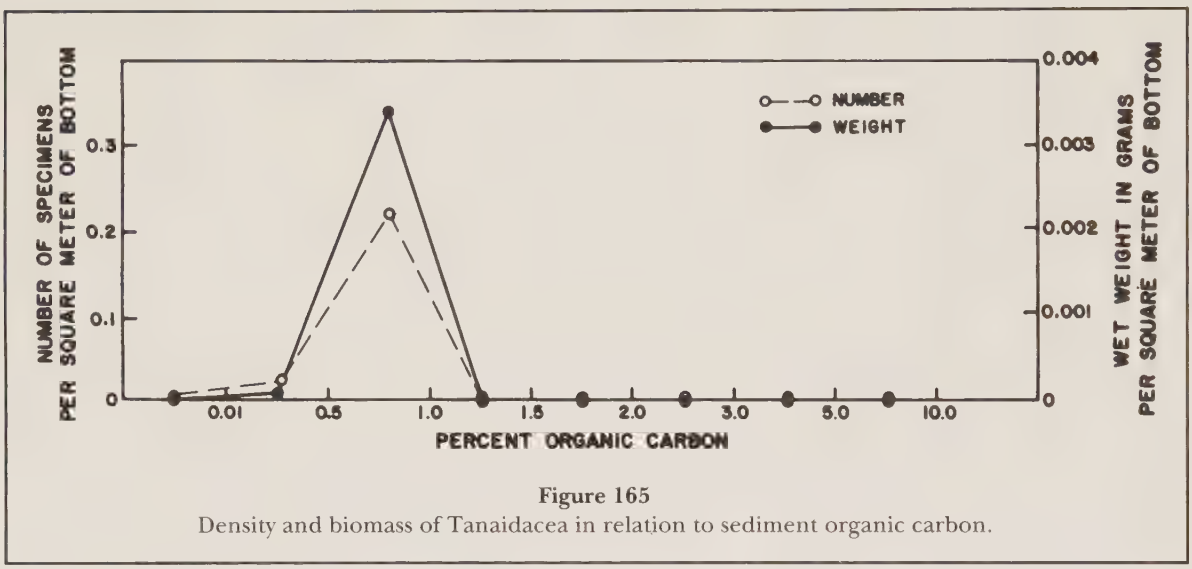


Figure 165
Density and biomass of Tanaidacea in relation to sediment organic carbon.

Relation to Sediment Organic Carbon

Tanaidaceans occurred only in areas of low organic carbon (Tables 26, 28, 30; Fig. 165). Density, biomass, and incidence of occurrence were all low in two organic carbon content classes (0.01–0.49 and 0.50–0.99%).

Isopoda—Isopods were moderately sparse but widely distributed throughout New England waters. Because of their limited abundance and small size they made up only a small portion of the total benthic fauna. They accounted for <1% of the total number of benthic animals and only 0.2% of the total biomass (Table 3).

Isopods in our samples ranged from 3 to 20 mm in length; the majority of specimens were approximately 10 to 15 mm long. Color of most specimens was translucent to light tan or medium brown.

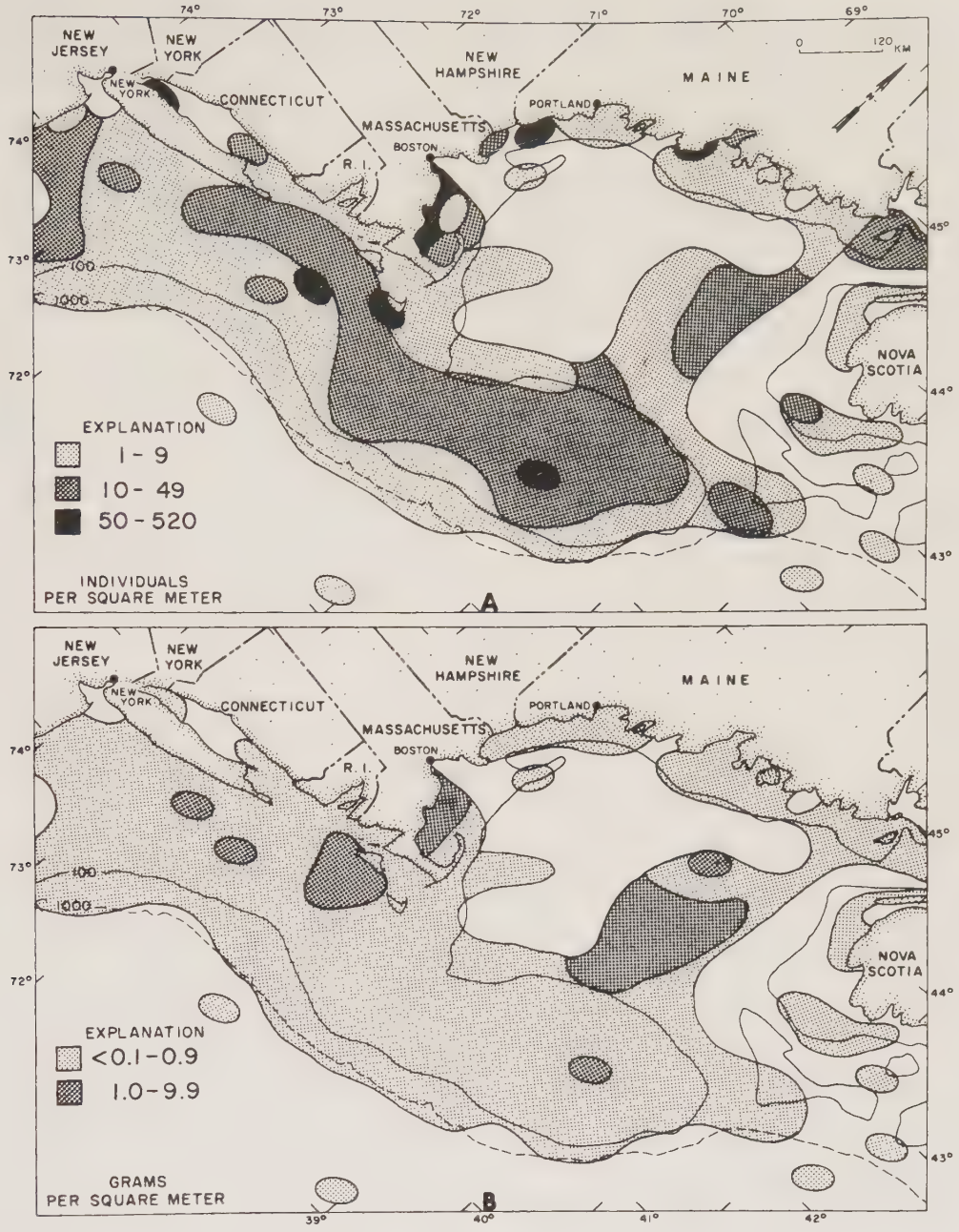
Approximately 13 species of isopods were represented in the collections, most of which belonged to the families Cirolanidae and Idoteidae. A new species, *Chiridotea arenicola* Wigley (1960a), was described from specimens found in collections from Georges Bank.

A large proportion of the specimens were adapted for burrowing in sand or for crawling on sandy or rocky substrates.

Isopods occurred in 390 samples (36% of total). Their density averaged 12.1/m^2 and their biomass averaged 0.29 g/m^2 (Table 5).

Geographic Distribution

Isopods were widely distributed over large portions of the study area (Fig. 166). They were especially common on the banks and in coastal regions. They were least common in the deeper portion of the western Gulf of Maine, in the vicinity of Nova Scotia, and on the continental shelf and rise. Densities between 10 and 50 indi-



ISOPODA

Figure 166

Geographic distribution of Isopoda: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

viduals/m^2 extended over large areas of the Gulf of Maine and Southern New England. High densities of 50 to 520 individuals/m^2 occurred in relatively few small areas. Average biomass was commonly less than 1 g/m^2, and the highest average biomasses were between 1 and 9.9 g/m^2.

Among the six standard geographic areas, isopods were most numerous (18 and 17 individuals/m^2) on Georges Bank and the Southern New England Shelf (Table 6; Fig. 167). Intermediate densities (3.9 and 9.5/m^2) were found in the Nova Scotia and Gulf of Maine areas. Low densities (1.0 and 1.3/m^2) occurred in the two slope areas.

The average biomass of isopods was small (0.4 g/m^2 or less) in all areas (Table 8; Fig. 167).

The quantitative geographic distribution of isopods was very similar to that of cumaceans (see Table 6). The

major difference was that cumaceans were twice as numerous as isopods, but the relative densities of the two groups corresponded rather closely. The geographic distributions of the two groups were also similar (see Fig. 154).

Frequency of occurrence of isopods in the samples was moderate (48% of the samples) on Georges Bank and the Southern New England Slope. In the other four geographic areas isopods occurred in 20 to 35% of the samples (Table 10).

Bathymetric Distribution

Isopods occupied a very wide depth range (5–3,820 m) and specimens were present in all eight depth classes (Table 11; Fig. 168). Densities were highest (22–38 individuals/m^2) in the two shallowest depth classes and decreased as water depth increased. Lowest density (0.4/m^2) was encountered in water depths between 1,000 and 2,000 m. In samples from the deepest strata (2,000–4,000 m) the density was 1.9/m^2.

Biomass values exhibited similar patterns in relation to water depth (Table 13; Fig. 168). The average biomasses of isopods were much higher (ranging from 0.15 to 0.66 g/m^2) in water depths less than 500 m than in deeper water where the average biomass ranged from only 0.01 to 0.02 g/m^2.

Frequency of occurrence of isopods was highest (46 to 69%) in samples from water depths ranging between 25 and 100 m. Occurrence rates were intermediate (12–20%) in samples from outer continental shelf and continental slope depths (100–2,000 m) and moderately high (43%) at depths greater than 2,000 m (Table 15).

Relation to Sediments

Isopods were found in all of the sediment types occurring in the study area (Table 16; Fig. 169) but were three to seven times more numerous (22.4 individuals/m^2) in sand substrates than in any other type of bottom. The average density of isopods in the other sediment types was fairly uniform, ranging only from 3 to 7/m^2.

The average biomass of isopods was highest (1.36 g/m^2) in till substrates (Table 18; Fig. 169). Also, as was the case

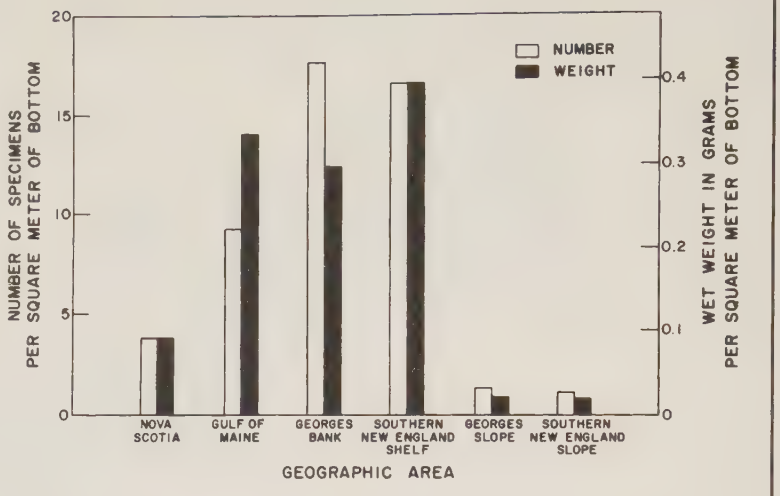


Figure 167
Density and biomass of Isopoda in each of the six geographic areas.

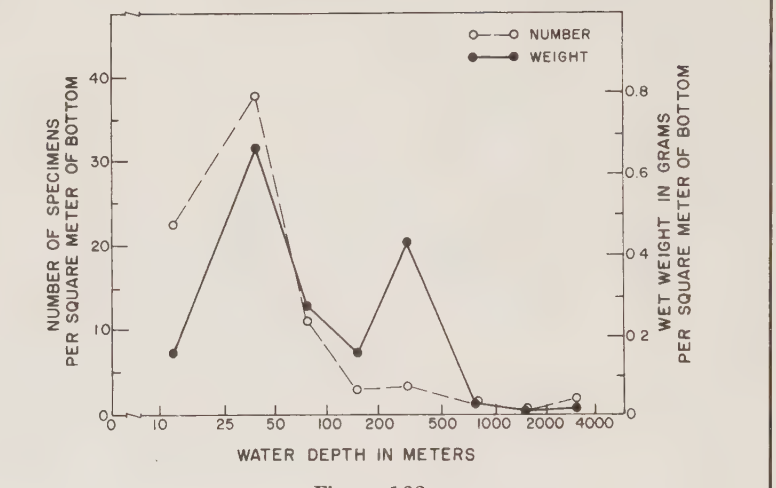


Figure 168
Density and biomass of Isopoda in relation to water depth.

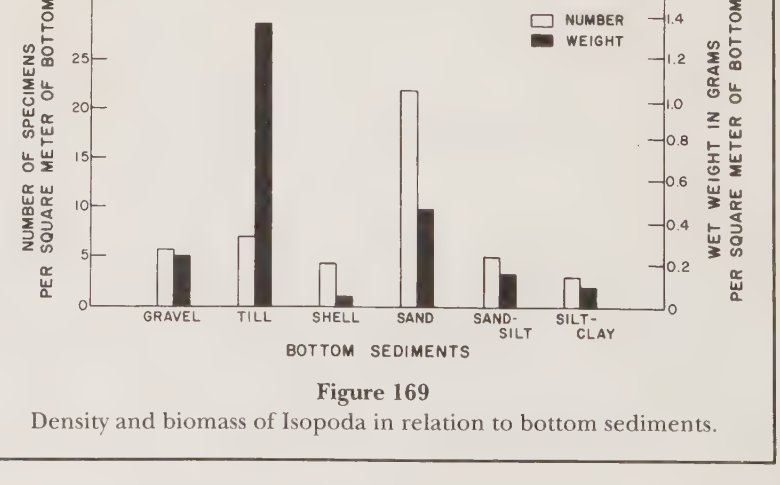


Figure 169
Density and biomass of Isopoda in relation to bottom sediments.

with density, the disparity between the highest and lowest biomass values was quite large. Average biomass (0.44 to 0.04 g/m^2) in the other five sediment types was nearly 3 to 30 times smaller than in till.

Frequency of occurrence of isopods in samples from the various sediment types reflected about the same quantitative distribution exhibited by density and biomass combined. Fifty percent or more of the samples from both till and sand contained isopods, whereas only 16 to 32% of the samples from the other sediment types yielded specimens (Table 20).

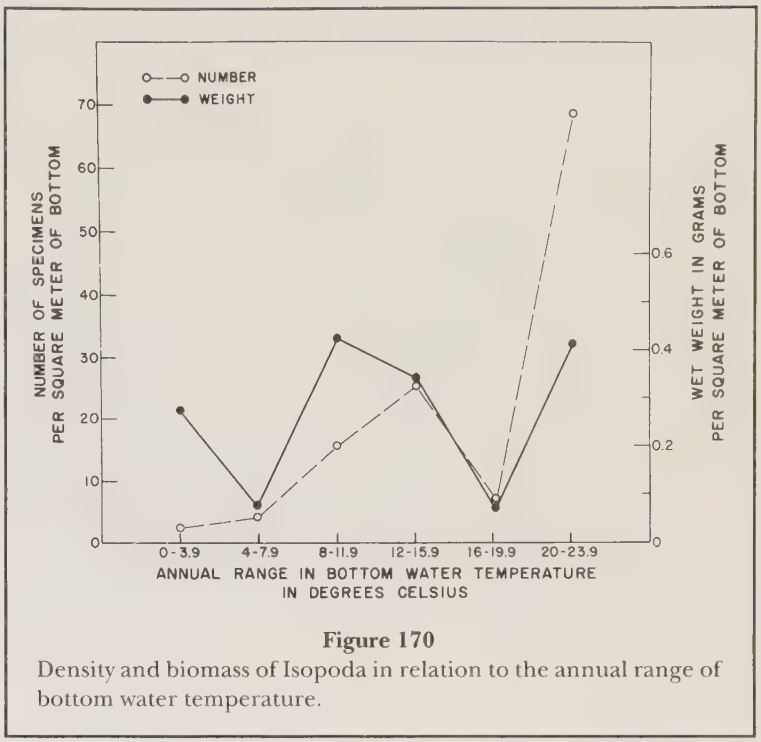


Figure 170
Density and biomass of Isopoda in relation to the annual range of bottom water temperature.

Relation to Water Temperature

Among the six temperature range classes two major concentrations of isopod density were detected (Table 21; Fig. 170). One concentration occurred in the broadest (20–23.9°C) temperature range class, which contained the highest density (67 individuals/m^2). The second concentration occurred where the temperature range was from 8 to 15.9°C. Isopod densities in this zone averaged 16 to 25/m^2. Over the remaining temperature ranges, average isopod densities were from 3 to 7/m^2.

Although the biomass of isopods was small in all temperature range classes, the quantities varied in approximately direct proportion to their density (Table 23; Fig. 170). Relatively large biomasses (0.34 to 0.42 g/m^2) occurred in the same temperature range classes as those for high density. Smaller quantities were present where the density was low.

Frequency of occurrence in each of the temperature range classes was moderate to moderately low. The occurrence rates varied directly with density and biomass values. Relatively high percentages of samples (43 to 61%) contained isopods in the intermediate and broadest temperature range classes. Relatively low occurrence rates (20 to 31% percent) were found in the other classes (Table 25).

Relation to Sediment Organic Carbon

Isopod density in the various organic carbon content classes exhibited a trend similar to that in relation to water temperature in that two major concentrations were detectable (Table 26; Fig. 171). The highest concentration (18 individuals/m^2) occurred in the next to highest content class (3.00–4.99% organic carbon); whereas, the second highest concentration (13/m^2) was in the class containing the lowest amounts of organic carbon detected (0.02–0.49%). Interestingly, a moderate density (9/m^2) of isopods occurred in areas of undetectable organic carbon. Lowest density (<1/m^2) occurred in the lower middle range (1.5–1.99%) of carbon content.

Biomass of isopods was negatively correlated to organic carbon content, tending to decrease as organic content increased (Table 28; Fig. 171). On the whole, biomass was relatively low, ranging from 0.27 to 0.03 g/m^2. Notable anomalies in the general trend occurred in the absence of measurable carbon (0.19 g/m^2) and in a comparatively sizeable (0.14 g/m^2) biomass in the content class that contained the lowest density (1.5–1.99%).

Frequency of occurrence of isopods in the samples in the organic carbon content classes was moderately high (47 and 25%) at the extreme ends of the range and intermediate (5 to 15%) in the intervening content classes (Table 30).

Amphipoda—Amphipods were exceedingly numerous and widely distributed throughout New England marine waters. They were the most abundant taxonomic group encountered in this study, forming 43% of the total number of individuals in the macrobenthos. Because of their small size, however, they did not contribute a correspondingly large share (2.3%) of the total standing crop (Table 3).

The amphipods collected included a wide variety of taxonomically diverse kinds (Dickinson et al., 1980; Dickinson and Wigley, 1981). We estimate that between 100 and 150 different species are represented in the samples. Four new genera and eight new species of amphipods were described, at least in part, from specimens collected during the present study. The following

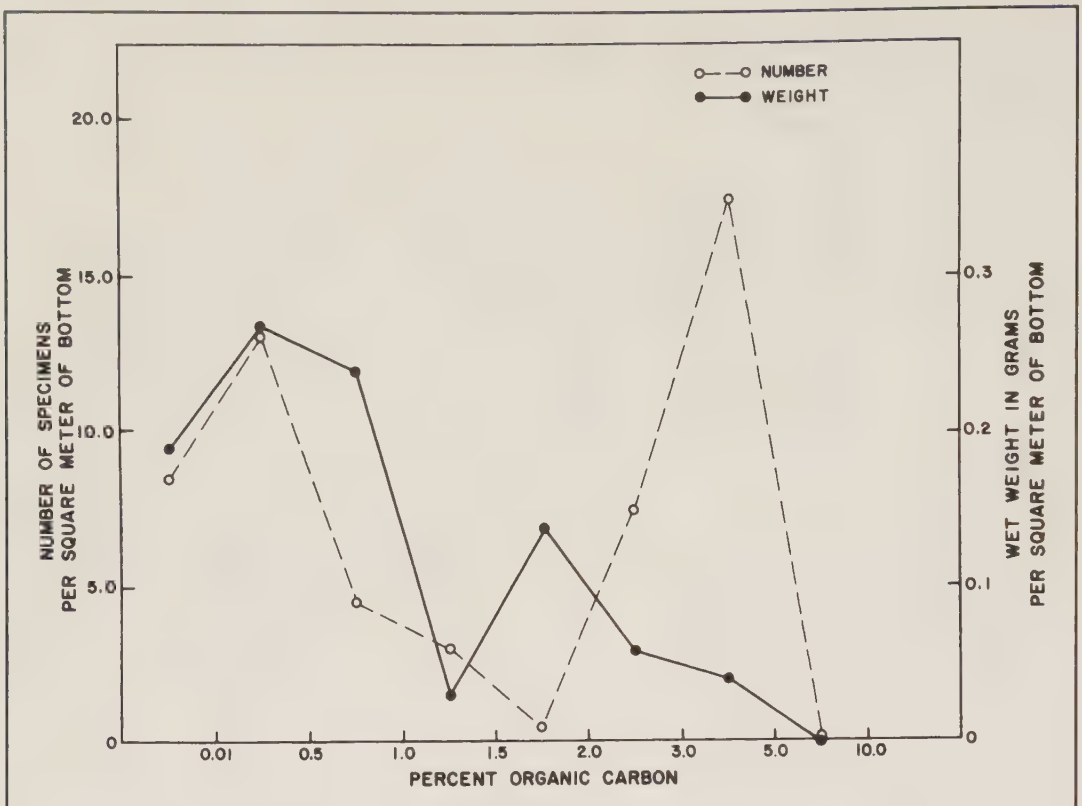


Figure 171
Density and biomass of Isopoda in relation to sediment organic carbon.

new forms were described by Edward L. Bousfield (1965), National Museum of Canada: *Protohaustorius wigleyi, Parahaustorius longimerus, P. holmesi, P. attenuatus, Pseudohaustorius borealis, Acanthohaustorius millsi, A. intermedius,* and *A. spinosus.* At least three suborders are represented in the collections: Gammaridea, Caprellidea, and Hyperiidea. Both the species and the number of individuals of the first group were considerably more numerous than in the latter two groups.

Body size of amphipods was somewhat limited. Small species, which were common in the families Metopidae and Stenothoidae, were 1 to 2 mm in length, or slightly more. The largest species in our collections, the caprellid *Aeginina longicornis,* had a body length of more than 2 cm. Gammaridea larger than 1.5 cm (*Casco, Maera,* and a few others) were uncommon.

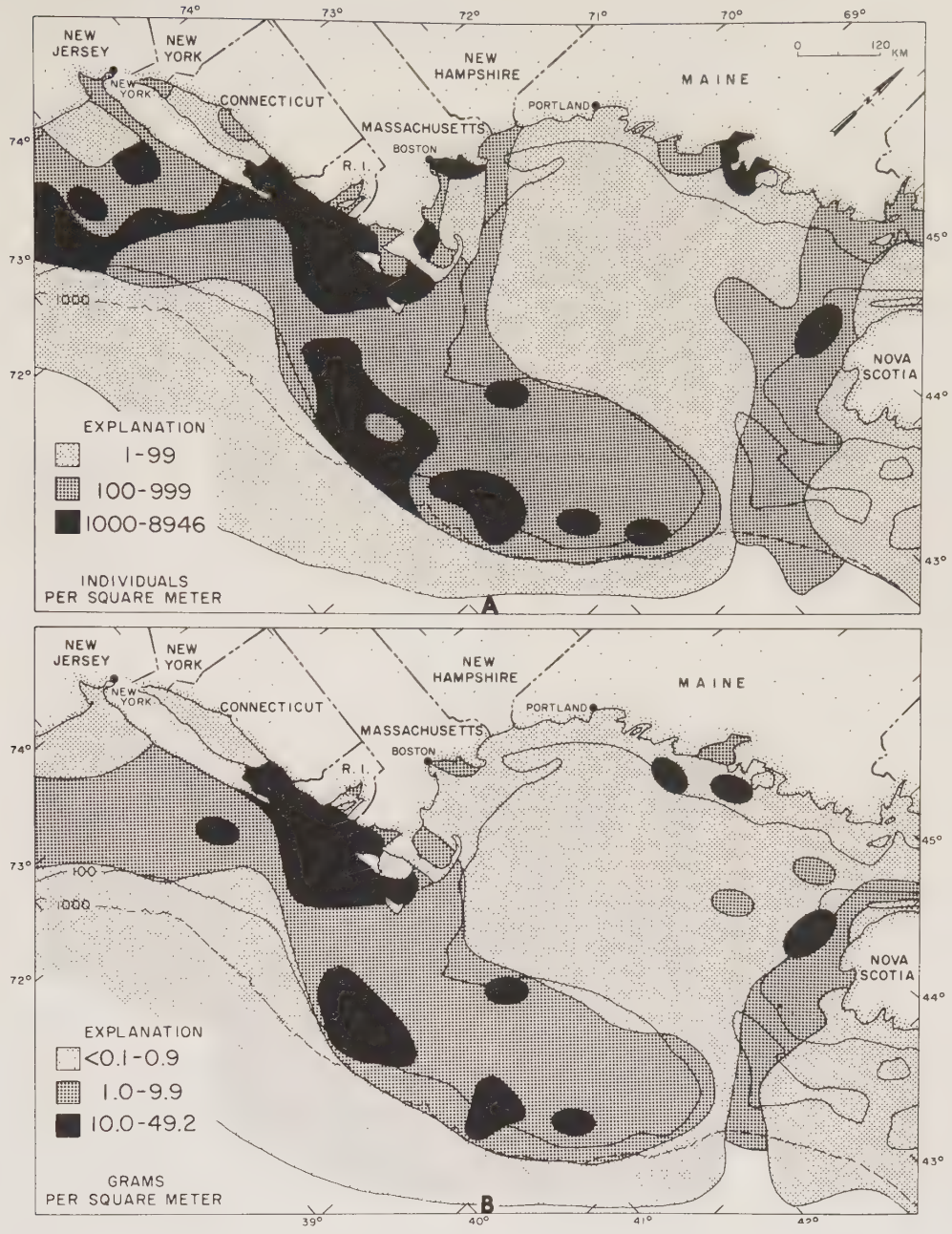
Color of amphipods ranged from light cream or nearly white (*Lysianopsis, Ampelisca,* and many others) to moderately dark brown (*Leptocheirus, Melita,* and others). No brightly colored specimens were detected. Some of the more colorful genera were *Stenothoe, Listriella,* and *Amphiporeia,* which have red eyes that contrast with the cephalon, and some members have contrasting colors on the thoracic and abdominal plates.

Quite a few species of New England gammaridean amphipods are tube dwellers. The tubes are usually elongate, cylindrical, or laterally flattened structures constructed of sand grains or clay particles cemented together. It may be significant that at least two of the most common genera (*Ampelisca* and *Unciola*) are tube dwellers. Also *Haploops,* which is one of the few amphipods that was relatively common in the deeper waters of the Gulf of Maine, is tubicolous.

Amphipods occurred in 862 samples (80% of total), their density averaged 656/m^2, and their biomass averaged 4.16 g/m^2 (Table 5).

Geographic Distribution

Amphipods were extensively distributed throughout the New England region (Fig. 172). They were particularly abundant on the continental shelf, except for the deeper parts of the Gulf of Maine and the southwestern part of the Nova Scotian shelf. Amphipods were an exceptionally abundant group and densities in the coastal areas and on the offshore banks commonly averaged between 100 and 1,000 individuals/m^2. High density (1,000 to 8,900 individuals/m^2) areas were not uncommon in this region. Densities of 1 to 100/m^2 were typical in the



AMPHIPODA

Figure 172

Geographic distribution of Amphipoda: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

deeper parts of the Gulf of Maine and on the continental slope and rise. The biomass of amphipods in the coastal areas and on the offshore banks generally averaged between 1 and 50 g/m^2. In the central Gulf of Maine and on the continental slope and rise, the biomass of amphipods averaged less than 1 g/m^2.

Two of the standard geographic areas, Georges Bank and the Southern New England Shelf, contained very high average densities (953 and 1,269 individuals/m^2, respectively) of amphipods (Table 6; Fig. 173). Three areas (Gulf of Maine, Georges Slope, and Nova Scotia) had intermediate densities (118 to 280/m^2). The South-

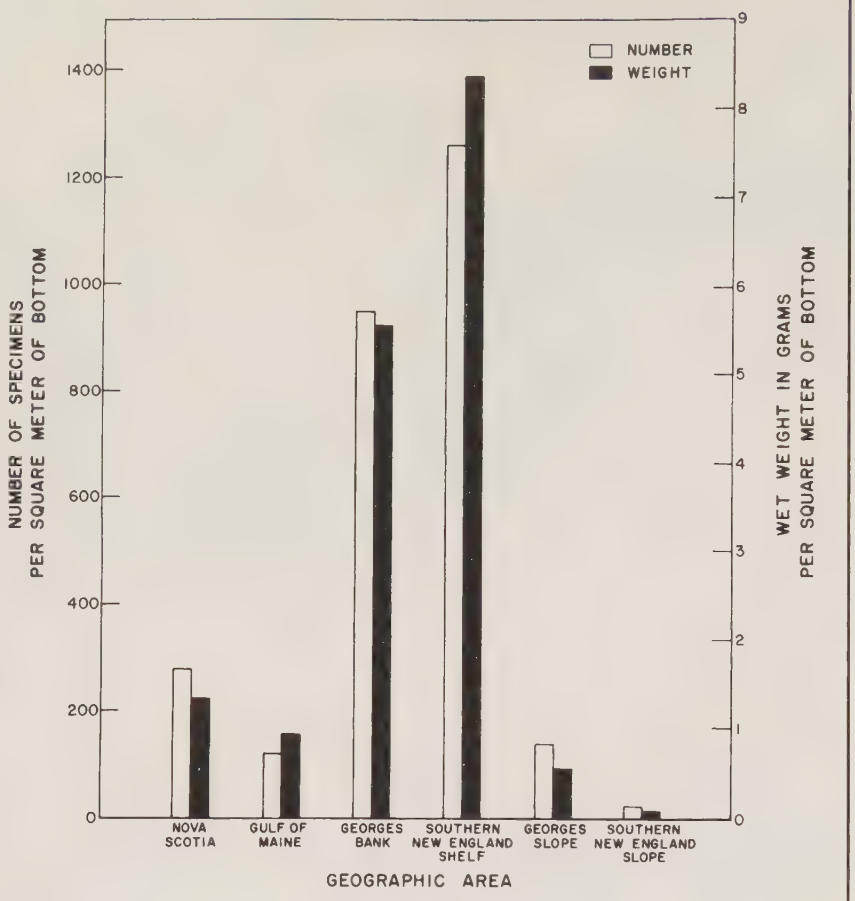


Figure 173
Density and biomass of Amphipoda in each of the six geographic areas.

ern New England Slope area yielded an average of only 17 amphipods/m^2.

Average biomass was very closely correlated with number of specimens and ranged from 8.34 g/m^2 in the Southern New England Shelf area to 0.08 g/m^2 in the Southern New England Slope area (Table 8; Fig. 173).

Frequency of occurrence of amphipods was generally high; they were found in 58 to 94% of the samples. In the three shallow shelf areas their occurrence ranged from 92 to 94% of the samples. Occurrence was lowest (58 to 73%) in the Gulf of Maine and the two slope areas (Table 10).

Bathymetric Distribution

Amphipods occurred at depths of 5 to 3,975 m. Their densities were highest on the continental shelf and decreased with increasing water depth (Table 11; Fig. 174). Usually high average densities (1,149 and 1,274 individuals/m^2) were encountered at depths between 25 and 100 m. In water depths greater than 100 m, amphipod densities dropped sharply. The average value for the lower continental slope area was 12/m^2, and on the continental rise their density declined to an average of only three specimens/m^2.

Biomass values revealed distribution patterns in relation to depth similar to those described above for density (Table 13; Fig. 174). At depths less than 100 m, the average biomass values were between 6 and 10 g/m^2. In water deeper than 100 m, a pronounced decline in biomass occurred; values ranged from 0.97.g/m^2 on the outer continental shelf to 0.02 g/m^2 on the continental rise.

Frequency of occurrence was moderate to high. In the shallow and moderately shallow water (0–100 m) amphipods occurred in 80 to 98% of the samples, but in deeper water they were present in 44 to 77% of the samples (Table 15).

Relation to Sediments

Amphipods were encountered in all of the different bottom types and revealed marked changes in density

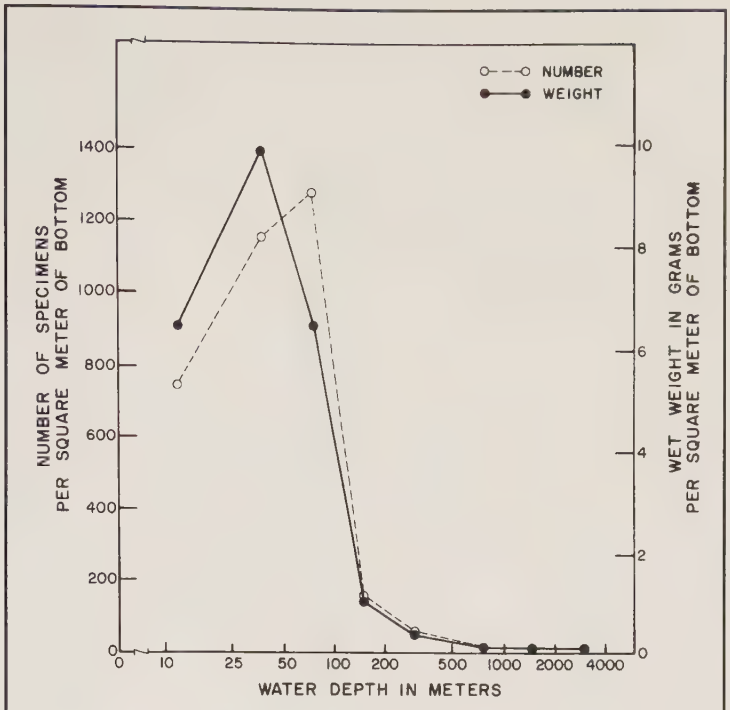


Figure 174
Density and biomass of Amphipoda in relation to water depth.

from one type to another (Tables 16, 17; Fig. 175). Density was exceptionally high (1,238 individuals/m^2) in sand and contributed over 56% of the total number of animals in this type of sediment. Density was moderately high in gravel; intermediate in sand-silt, till, and shell; and relatively low (23/m^2) in silt-clay.

Biomass trends were the same as those for density (Table 18; Fig. 175). Sand sediments contained the largest biomass, an average of 7.7 g/m^2. Intermediate quantities (0.5 to 3.4 g/m^2) were present in gravel, till, shell, and sand-silt. The lowest biomass (0.18 g/m^2) was found in silt-clay.

The occurrence of amphipods in different types of sediments ranged from very high to moderate. It was high to very high (93 to 100%) in sand, shell, and gravel types; intermediate in till and sand-silt; and moderate (51%) in silt-clay (Table 20).

Relation to Water Temperature

Amphipods occupied the entire spectrum of temperature range variations occurring in the study area (Table 21; Fig. 176). Highest average density (1,372 individuals/m^2) was encountered where the temperature was intermediate (8°–11.9°C). Densities were moderately high (598–809/m^2) in areas where the range in temperature was broad, but were substantially lower (58–311/m^2) where the temperature range was nil or small.

Amphipod biomass in relation to temperature range paralleled the same trends as those revealed by numerical density (Table 23; Fig. 176). Greatest biomass (8.1 g/m^2) occurred in an intermediate temperature range class (8°–11.9°C). Moderate values occurred in adjacent broader and narrower range classes. The smallest (0.41 g/m^2) biomass was found where the temperature range was less than 4°C.

The frequency of amphipods in our samples was moderate to high in all temperature range classes (Table 25). The highest rates of occurrence (92 to 97%) were encountered where the temperature range was moderate. Somewhat lower incidence rates occurred where the ranges in temperature were slightly narrower and slightly broader. Lowest occurrence rates prevailed in those areas where the temperature range was lowest (less than 4°C) and highest (more than 20°C).

Relation to Sediment Organic Carbon

Amphipods occurred in all sediments containing organic carbon (Table 26; Fig. 177). Two abundance peaks were clearly evident. Densities were very high (between 1,000 and 1,256 individuals/m^2) in both low (0.01–0.49%) and high (3.00–4.99%) concentrations of organic carbon and were much lower (24 to 164/m^2) where organic carbon content was between these ex-

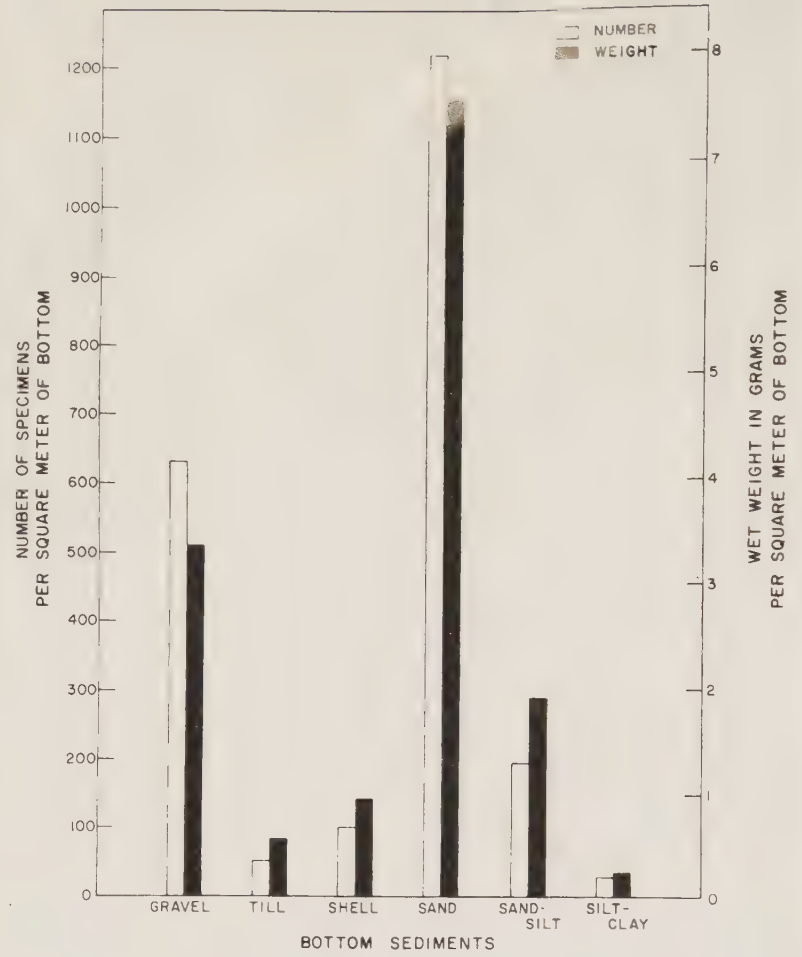


Figure 175
Density and biomass of Amphipoda in relation to bottom sediments.

tremes. Lowest density occurred in the absence of measurable organic carbon.

Biomass followed the pattern established by density (Table 28; Fig. 177). Biomass was high (8.3 to 5.3 g/m^2) at high and low carbon concentrations, fell to much lower levels (0.2 to 1.8 g/m^2) in intermediate levels, and was lower still where carbon was absent or at the highest levels measured.

Frequency of occurrence was high (93 to 100% of the samples) in the organic carbon content classes containing the lowest and highest concentrations measured but dropped to moderate levels (49 to 72%) in all other classes (Table 30).

Mysidacea—Mysids constituted a minor portion of the total benthos, 0.2% of the number of individuals and less than 0.1% of the biomass (Table 3). They were small in size, their geographic distribution was limited, and their numerical density was generally low. The average number of specimens usually was less than 5/m^2 and average biomass less than 0.01 g/m^2. Some species of mysids characteristically make diurnal excursions from the sea bottom to the upper water layers, at which time they become members of the plankton community; however, when they retreat to the ocean floor to feed or to excavate in the bottom sediments, they are considered an integral part of the benthos. Since bottom grabs do not sample mysids well, our data should not be taken as indicative of actual distribution or abundance.

Individual specimens in our collections ranged in body length from 3 to 12 mm. The large inshore species *Mysis stenolepis* and *Praunus flexuosus* were not present in our quantitative samples.

The color of the majority of specimens was white or translucent with small areas of brownish to nearly black

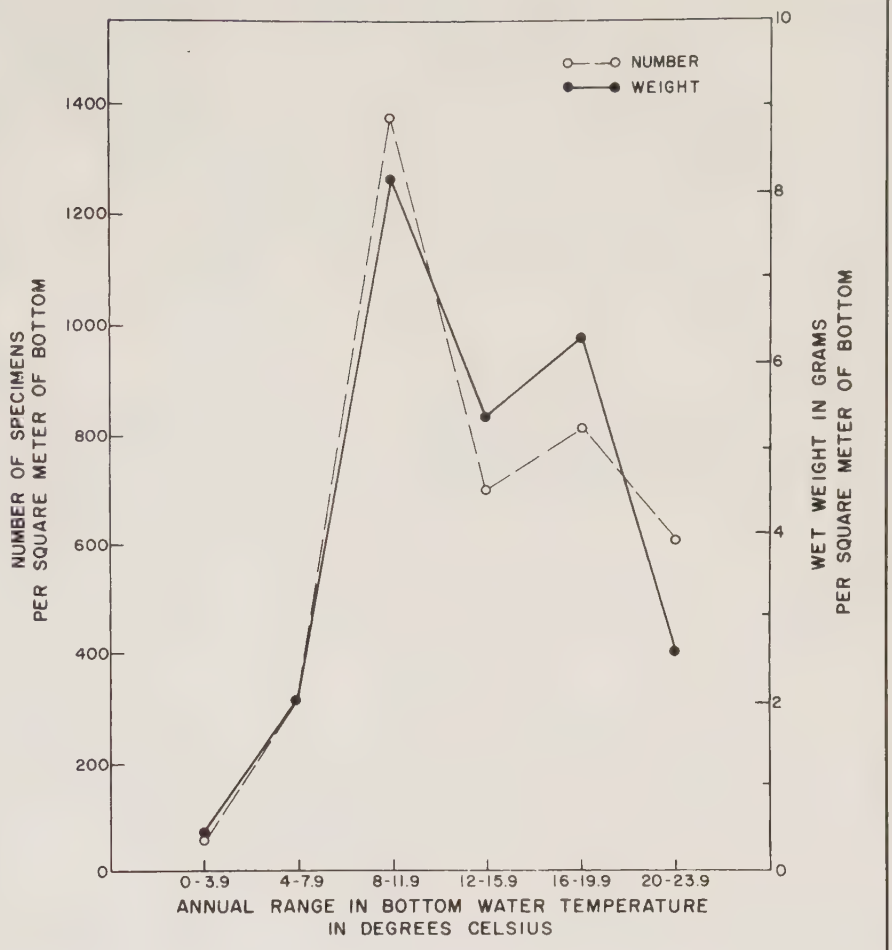


Figure 176
Density and biomass of Amphipoda in relation to the annual range of bottom water temperature.

pigmentation on the body and appendages. The eyes of most species were brownish-black. The most colorful members of the group were specimens of *Erythrops erythrophthalma*, which had red eyes and yellow and orange color patches on the body.

Mysids occurred in 41 samples (nearly 4% of the total). Their density averaged 2.5/m^2, and biomass averaged 0.01 g/m^2 (Table 5).

Geographic Distribution

Mysids were sparsely distributed in the study area occurring in widely separated patches mainly along the Southern New England, Long Island, and New Jersey shores (Fig. 178), and on Georges Bank. Two small enclaves also occurred inshore on the central Maine coast and in the mouth of Saint Mary Bay in western Nova Scotia.

Average density was low (1–49 individuals/m^2) in all localities except for two small patches of moderate density (50–99/m^2) south of the northern edge on Georges Bank and a patch of moderately high density, between 100 and 187 individuals/m^2, on south-central Georges Bank.

Mysid biomass was typically low (<0.1–0.9 g/m^2) in all areas of occurrence except for one small patch in the region of highest density where biomass barely exceeded 1 g/m^2.

Georges Bank was dominant among the standard geographic areas in both measures of mysid abundance (Tables 6, 8; Fig. 179), containing an average density and biomass of 10.6 individuals/m^2 and 0.06 g/m^2, respectively. The other geographic areas contained significantly lower amounts, ranging from 10 to 100 times less in terms of density and 6 times less in terms of biomass.

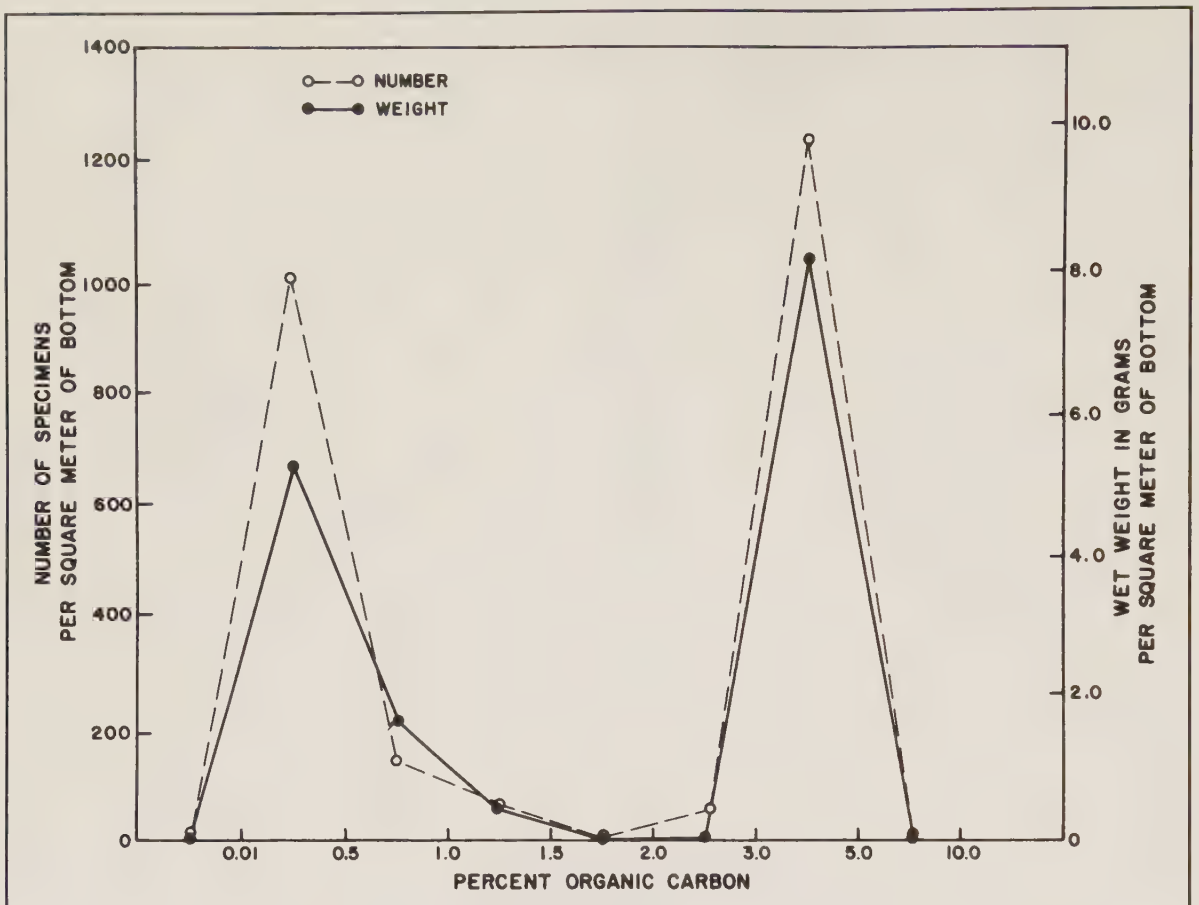


Figure 177
Density and biomass of Amphipoda in relation to sediment organic carbon.

Frequency of occurrence of mysids in samples was low in all areas ranging only from 1 to 10% (Table 10). Georges Bank had the highest occurrence frequency.

Bathymetric Distribution

Mysids occurred in the somewhat limited depth range of 9 to 292 m. They were most abundant (densities of 3.8 to 6.5 individuals/m^2) at depths less than 100 m (Table 11; Fig. 180). At depths greater than 100 m, their density was only 0.1 or less/m^2.

Biomass, although very small, revealed a rather constant diminution in quantity from shallow to deep water (Table 13; Fig. 180).

Mysids occurred in 13% of the samples from the shallowest depth class, and their rate of occurrence dropped with increasing water depth to 1% or less in the deepwater classes (Table 15).

Relation to Sediments

Mysids were found in four of the six bottom sediment types (Table 16; Fig. 181). Their density (5 individuals/m^2) in sediments composed of sand was substantially higher than in the other sediment types. In gravel, sand-silt, and silt-clay the densities were less than 1/m^2.

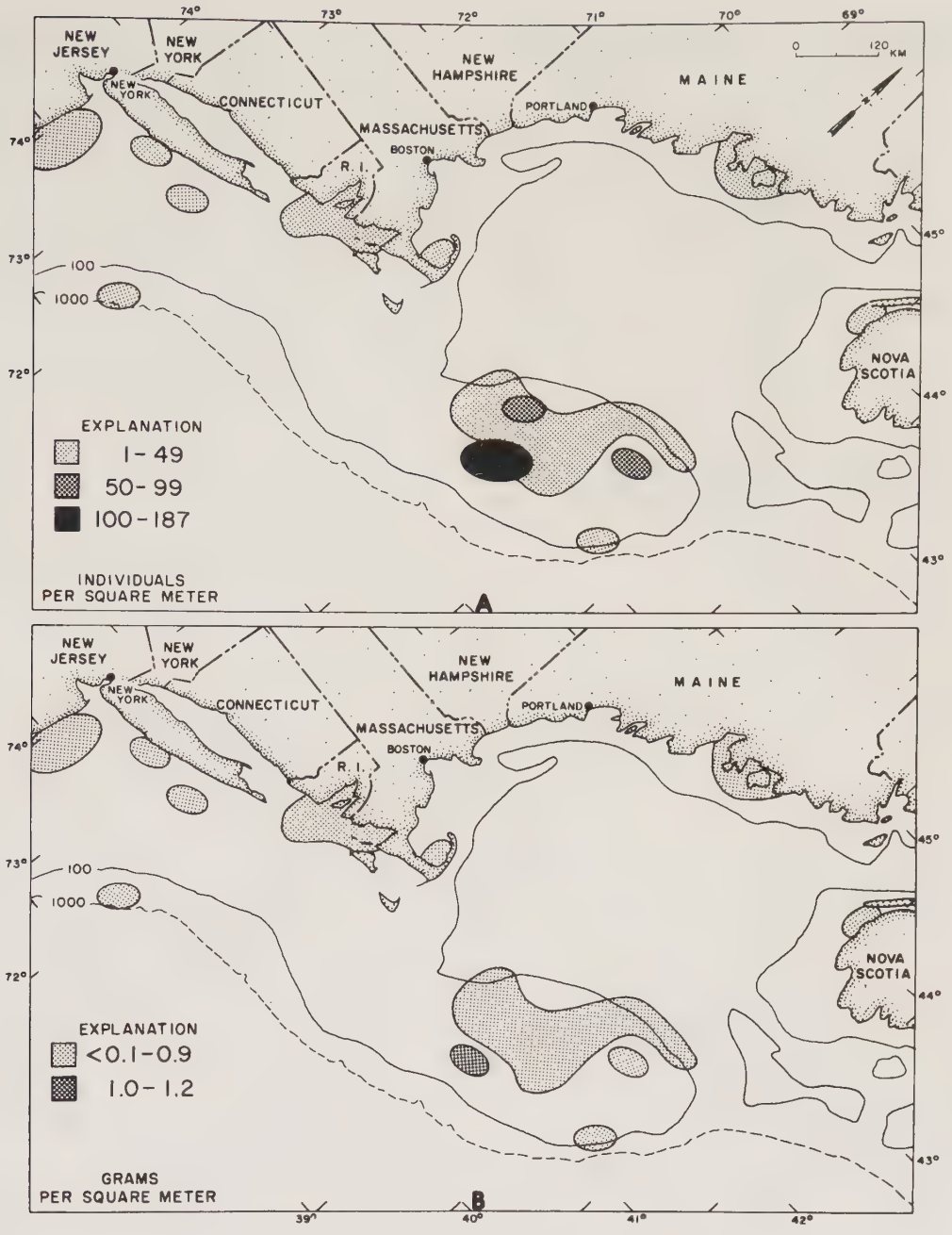
Biomass was very low (0.02 g/m^2) even in sand sediments where mysids were most abundant (Table 18; Fig. 181). Values for the other bottom types were 0.01 g or less/m^2.

Mysids were present in a higher proportion of the samples (6%) from sand sediments than from the other bottom types (Table 20).

Relation to Water Temperature

Mysids exhibited a general trend of increasing in both density and biomass as the annual range in temperature broadened (Tables 21, 23; Fig. 182). Average numerical density increased from <0.1/m^2 where the temperature range was <4°C, to 6.1/m^2 in localities where the temperature range was over 20°C. Biomass ranged from <0.01 to only 0.02 g/m^2.

Frequency of occurrence values varied in a similar, but more consistent, manner to those of density and biomass. The percentage of samples yielding specimens



MYSIDACEA

Figure 178

Geographic distribution of Mysidacea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

ranged from less than 1% in the lowest range class to 18% in the highest range class (Table 25).

Relation to Sediment Organic Carbon

Mysids occurred in four of the eight organic carbon content classes (Table 26; Fig. 183). Average densities (ranging from 0.8 to 1.8 individuals/m^2) were quite similarly distributed among the four classes, exhibiting a bimodal trend, one in the lower carbon content classes (between 0.01 and 0.99%) and the other in the intermediate (1.5 to 2.99%) classes.

Biomass values were uniformly low (0.01 g/m^2) in all organic carbon classes in which they occurred (Table 28; Fig. 183).

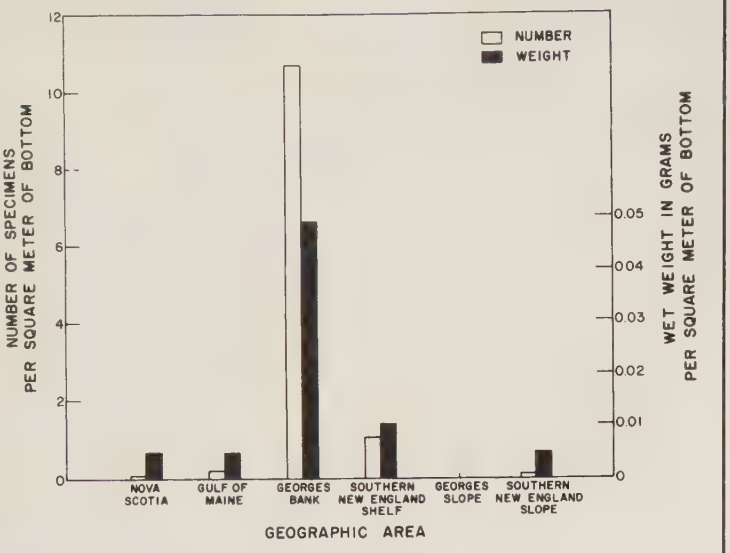


Figure 179
Density and biomass of Mysidacea in each of the six geographic areas.

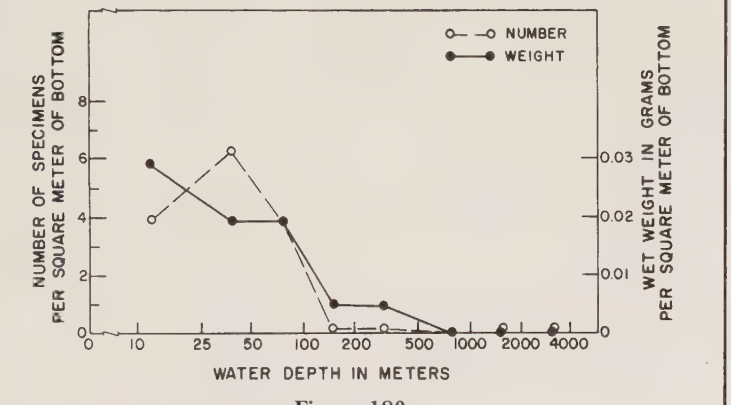

NUMBER
WEIGHT
NUMBER OF SPECIMENS PER SQUARE METER OF BOTTOM
WET WEIGHT IN GRAMS PER SQUARE METER OF BOTTOM
WATER DEPTH IN METERS

Figure 180
Density and biomass of Mysidacea in relation to water depth.

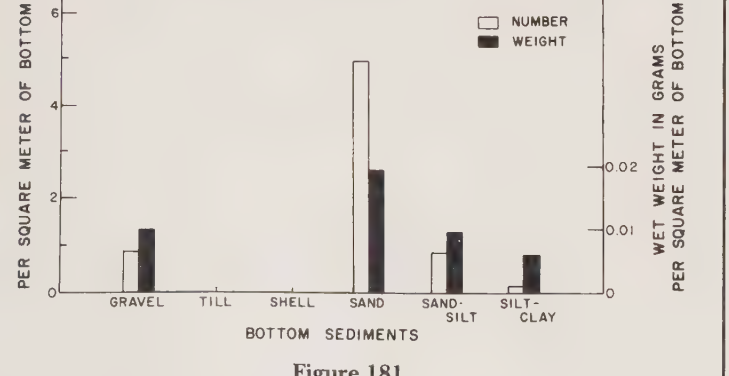


Figure 181
Density and biomass of Mysidacea in relation to bottom sediments.

Frequency of occurrence of mysids was higher (7 and 8%) in the intermediate carbon content classes than in the lower ones (3 and 5%) in which they occurred (Table 30).

Decapoda—Decapods, although well represented in terms of the number of taxa that were found in our quantitative samples (two suborders and three sections contained 24 genera and 34 species, Table 4), did not rank as highly in their contributions to the total number of specimens (0.5%), or to total biomass (0.8%) (Table 3). The apparent poor showing of the class, the largest among all classes of crustaceans, is misleading, precisely because of the large size and mobility of many of the representative species. These large, highly mobile forms are more effectively sampled by qualitative gear types, such as dredges and trawls, than by quantitative grab samplers. Thus the estimates of density and biomass presented in this report, for this class of crustaceans, should be considered to be very conservative at best. Indeed, the taxonomic list of decapods obtained by means of qualitative sampling gears in our databases is considerably more expansive than the one included here in Table 4. Nevertheless, the quantitative data reported in our report contain a fair representation of the major forms present in the region and constitute the most extensive and complete set (known to us) upon which to base our estimates.

Decapods were not found in most of the Gulf of Maine. For the most part, they are restricted to the Southern New England continental shelf and upper slope and to Georges Bank; some occurred on the western portion of the Nova Scotia shelf and the western basin of the Gulf of Maine. Average densities were low, ranging from 1 to 49 individuals/m^2, over most of their range in the study area. Size of captured specimens tended to be smaller than the overall average for this class, reflecting the bias imparted by the relatively small area sampled by the quantitative grabs used in our study. The smaller members of this group were less adroit at avoiding capture. The average size of caridian shrimps ranged from 20 to 40 mm; occasional larger specimens (40–60 mm) were captured. The latter were usually representatives of more sedentary, less active taxa, such as the burrowing sand shrimp *Crangon septemspinosus*. Average anomuran size ranged between 4 and 20 mm carapace length. Most frequently captured were representatives of the relatively

slow-moving pagurid hermit crabs. Size of brachyuran crabs averaged between 15 and 20 mm carapace width; the two species of *Cancer* did provide some larger specimens in the 50 to 60 mm range, and *Pinnixa* spp. provided some of the smaller specimens in the 5 to 6 mm range.

Colors of decapods in our samples ranged from the nearly transparent or translucent white of *Crangon* to the dark reddish browns and blacks of *Hyas*. A veritable spectrum of colors was represented between these extremes, ranging from the delicate flesh and pink hues of the pandalid shrimps, to the tans, greens, blues, and grays and muted reds of the pagurid and brachyuran crabs. Most colorful were the bright red-orange *Geryon quinquedens*.

The decapods as a group are similar to bivalves in providing a broad spectrum of prey to a variety of predators. In addition to man, whose harvests of lobsters, shrimps, and crabs are well known, many other marine animals (including other invertebrates, mammals, birds, and fishes) depend on decapod prey for a substantial portion of their sustenance.

Decapods occurred in 246 samples (23% of the total). Their density averaged 8 individuals/m^2, and their biomass 1.32 g/m^2 (Table 5).

Geographic Distribution

The most striking feature of decapod distribution revealed by our samples was their apparent absence from large portions of the Gulf of Maine (Fig. 184). This artifact is due primarily to sampling gear bias since, traditionally, this region has been well known for the high annual yields of lobsters and shrimps. However, low densities were recorded from the northeast corner of the Gulf at the entrance to the Bay of Fundy, the Western Basin section north of Great South Channel, and some inshore localities. Low densities (1–49 individuals/m^2) also prevailed over most of their range elsewhere on the continental shelf in the study area. Moderate (50–99/m^2) and high (100–266/m^2) average densities were restricted to small patches on Georges Bank and in Nantucket and Vineyard Sounds and at the head of Long Island Sound.

Average biomass of decapods was low (<0.1 to 9.9 g/m^2) over the major portion of their range; there were only a few small patches of moderate (10–50 g/m^2)

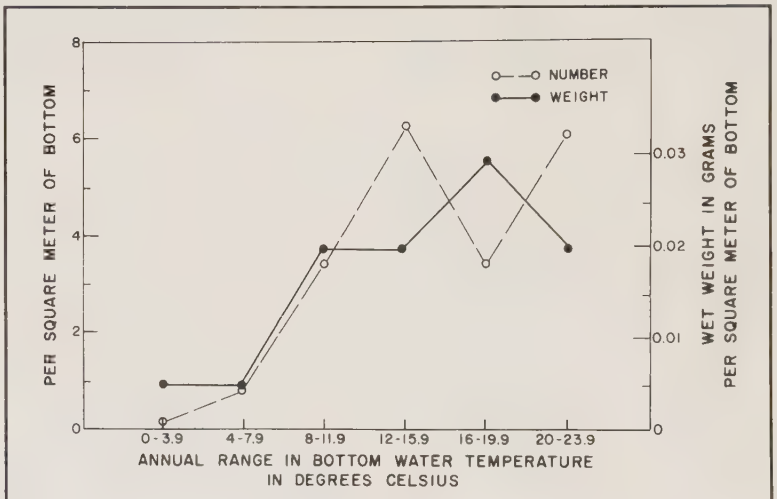


Figure 182

Density and biomass of Mysidacea in relation to the annual range of bottom water temperature.

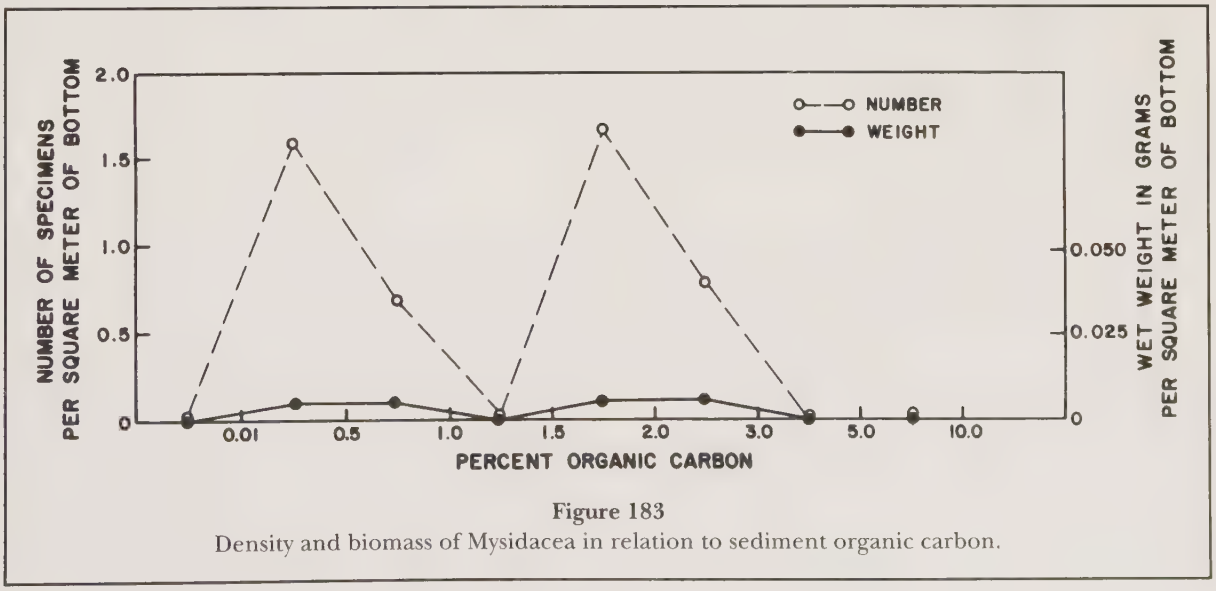
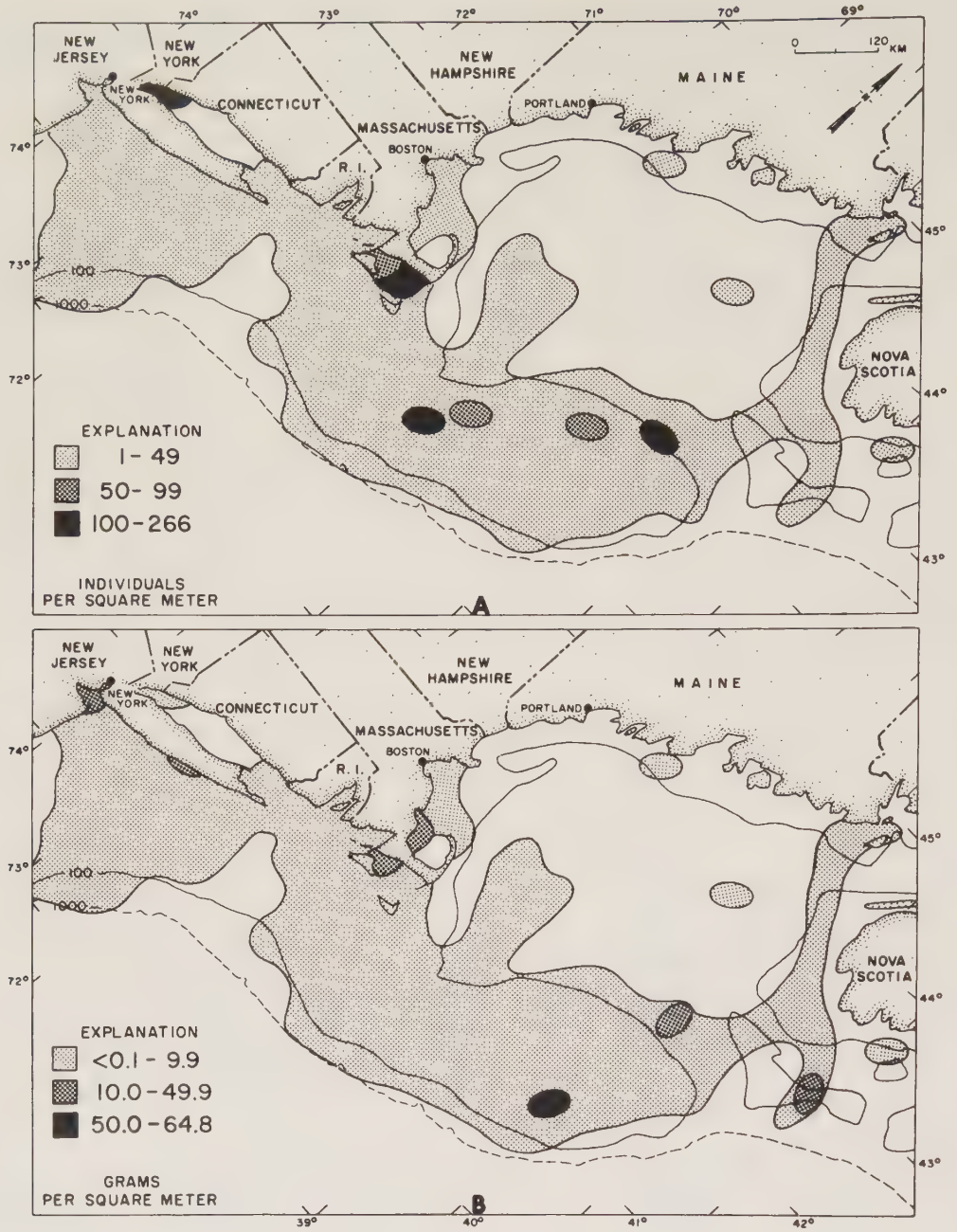


Figure 183

Density and biomass of Mysidacea in relation to sediment organic carbon.



DECAPODA

Figure 184

Geographic distribution of Decapoda: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

biomass, mostly in inshore regions near Cape Cod and Long Island. One small area of moderately high biomass (50–65 g/m^2) occurred on the southeast part of Georges Bank.

Decapods occurred in five of the six standard geographic areas; they were absent only in the Georges Slope area. Highest average density (22/m^2) occurred on Georges Bank followed by significantly lower densities on the Southern New England Shelf and off Nova Scotia (9 and 2/m^2, respectively). Density was below 1/m^2 in the Gulf of Maine and on the Southern New England Slope (Table 6; Fig. 185).

Average biomass ranged from slightly over 3 g/m^2 on Georges Bank to 0.02 g/m^2 on the Southern New England Slope (Table 8; Fig. 185). In the other areas, biomass ranged from 0.6 to slightly over 2 g/m^2.

Frequency of occurrence of decapods in the samples was moderately high on Georges Bank, Southern New England Shelf, and off Nova Scotia, ranging from 46 to 18% (Table 10). Their occurrence in samples from the Gulf of Maine and Southern New England Slope was considerably lower, 6 and 3%, respectively.

Bathymetric Distribution

Decapods were almost wholly restricted to water depths of less than 500 m and showed a general trend of diminishing in abundance as water depth increased (Table 11; Fig. 186). Average density was highest (18/m^2) in the shallowest depth-range class (0–24 m) and dropped to 50% and less of this value in the continental shelf depth classes between 25 and 200 m. Density in the upper slope depth class (200–499 m) was low (0.3/m^2) and very low (0.1/m^2) in the only deepwater depth class (1,000–1,999 m) in which they occurred.

Average biomass generally followed the trend established for density (Table 13; Fig. 186). In the shallow-water depth class, average biomass was nearly one and one half to three times (3.3 g/m^2) higher than that in the continental shelf depth classes where it ranged from 1.1 to 2.1 g/m^2. Biomass was 0.61 g/m^2 in the upper slope depth class (200–499 m) but only 0.03 g/m^2 in the deepest class in which decapods occurred (1000–1999 m).

Decapod frequency of occurrence in the samples was fairly uniform at moderate levels (35 to 39%) in the three depth classes <99 m, moderately low (13%) in the shelf edge class, and low (3 and 4%) in the other two classes they occupied (Table 15).

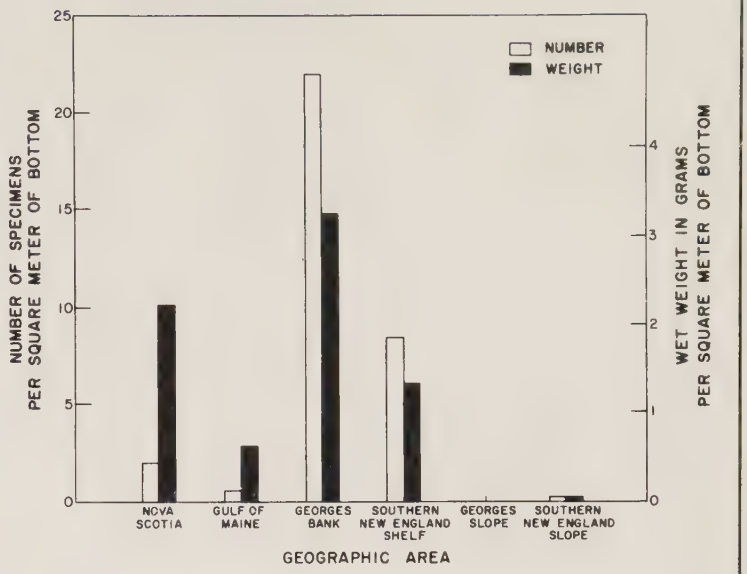


Figure 185
Density and biomass of Decapoda in each of the six geographic areas.

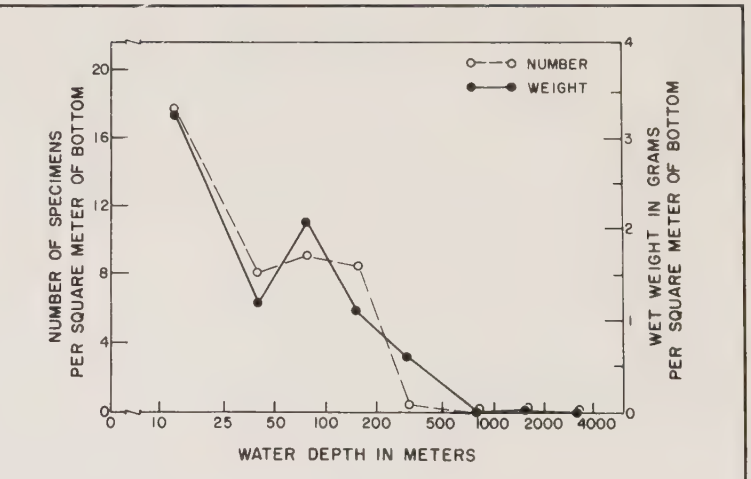


Figure 186
Density and biomass of Decapoda in relation to water depth.

Relation to Sediments

Decapods were present in all sediment types except till. Both density and biomass diminished with decreasing sediment particle size (Tables 16, 18; Fig. 187). Gravel bottoms contained the greatest average number (24/m^2) of decapods as well as greatest biomass (5.56 g/m^2). A drop in density occurred in shell and sand, each of which yielded an average of 9/m^2, nearly three times fewer decapods, but biomass diminution was not as dramatic in shell which contained an average of 4.78 g/m^2; however, sand contained nearly five times less biomass (1.16 g/m^2) than gravel. Sand-silt and silt-clay, the finest sediments, yielded lower density and biomass.

Frequency of occurrence of decapods was moderate and uniform in samples in gravel, shell, and sand, ranging from 33 to 37%, but was relatively low in sand-silt and silt-clay, 7 and 4%, respectively (Table 20).

Relation to Water Temperature

Average density and biomass of decapods showed a tendency to increase with broadening temperature range to

19.9°C; beyond this, in the 20.0–23.9°C range class, both measures declined (Tables 21, 23; Fig. 188). Average density and biomass (0.9/m^2 and 0.47 g/m^2, respectively) were lowest in the narrowest temperature range class (0–º3.9°C) and generally increased with broadening temperature range, peaking at 23.2/m^2 and 4.26 g/m^2 in the 16.0–19.9°C range class. Intermediate values of both measures occurred where the temperature range was broadest.

The frequency of occurrence of decapods in the samples in the various temperature range classes parallels the trend established for density and biomass, ranging from 6% in the narrowest range class to 53% in the 16–9.9°C class, and dropping to intermediate (18%) levels in the broadest range class (Table 25).

Relation to sediment organic carbon

Decapods were absent in areas where no measurable organic carbon occurred in the sediments, as well as in areas with the highest recorded amounts. They were present in the five organic carbon content classes between 0.01 and 2.99% where average density and biomass described U-shaped distributions (Tables 26, 28; Fig. 189). Average density ranged from nearly 8 to 0.5 individuals/m^2 and average biomass from 4.15 to 0.30 g/m^2. Values were highest at the extremes of the carbon content classes in which they occurred and fell to the lowest levels in the middle carbon content classes, slightly biased toward the higher end.

Frequency of occurrence of decapods in the samples described a distribution similar to density and biomass. Occurrence was moderate, ranging from 4 to 32%, but in this instance was biased slightly toward the lower end of the content range (Table 30).

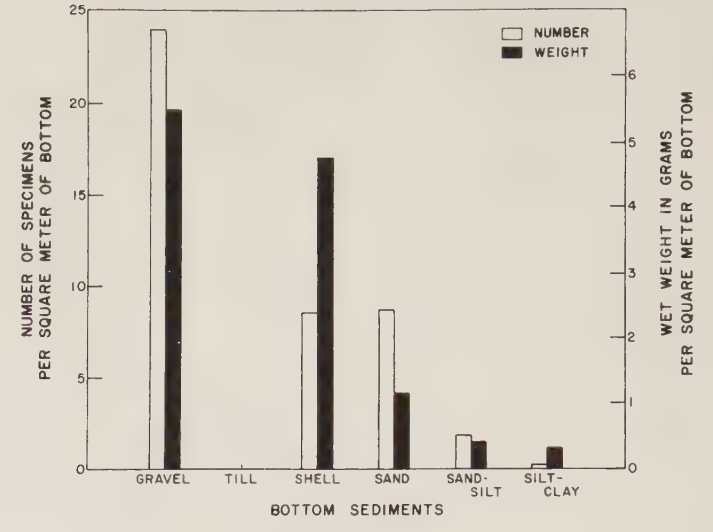


Figure 187

Density and biomass of Decapoda in relation to bottom sediments.

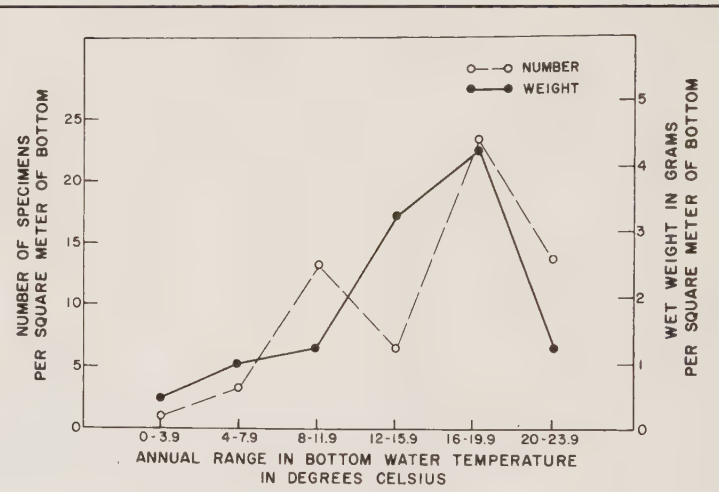


Figure 188

Density and biomass of Decapoda in relation to the annual range of bottom water temperature.

Bryozoa

Bryozoans are sessile colonial animals most frequently found attached to rocks, shells, ship bottoms, pilings, firm outer surfaces of other animals, and other similar hard substrates. Their distribution in the study area was somewhat patchy owing to their requirement for a firm substrate and moderate to strong water currents. The currents transport to them their main food supply, minute plankton, principally diatoms.

These organisms contribute a significant number (more than one hundred) of species to the New England benthic fauna. The majority of these species belong to the class Gymnolaemata, order Cheilostomata. The calcareous encrusting forms were especially numerous, but the chitinous foliaceous types were usually the largest specimens encountered.

Although the Bryozoa constitute a major phylum in species diversity and are a major contributor to the biomass in certain localized habitats, their small size and patchy distribution rather severely limited their contribution to the total benthic fauna. In terms of numerical density, ectoprocts made up 1% of the total fauna and contributed only 0.7% of the total biomass (Table 3).

Bryozoans occurred in 119 samples (11% of total). Their density averaged 15.7/m^2. Their biomass averaged 1.29 g/m^2 (Table 5).

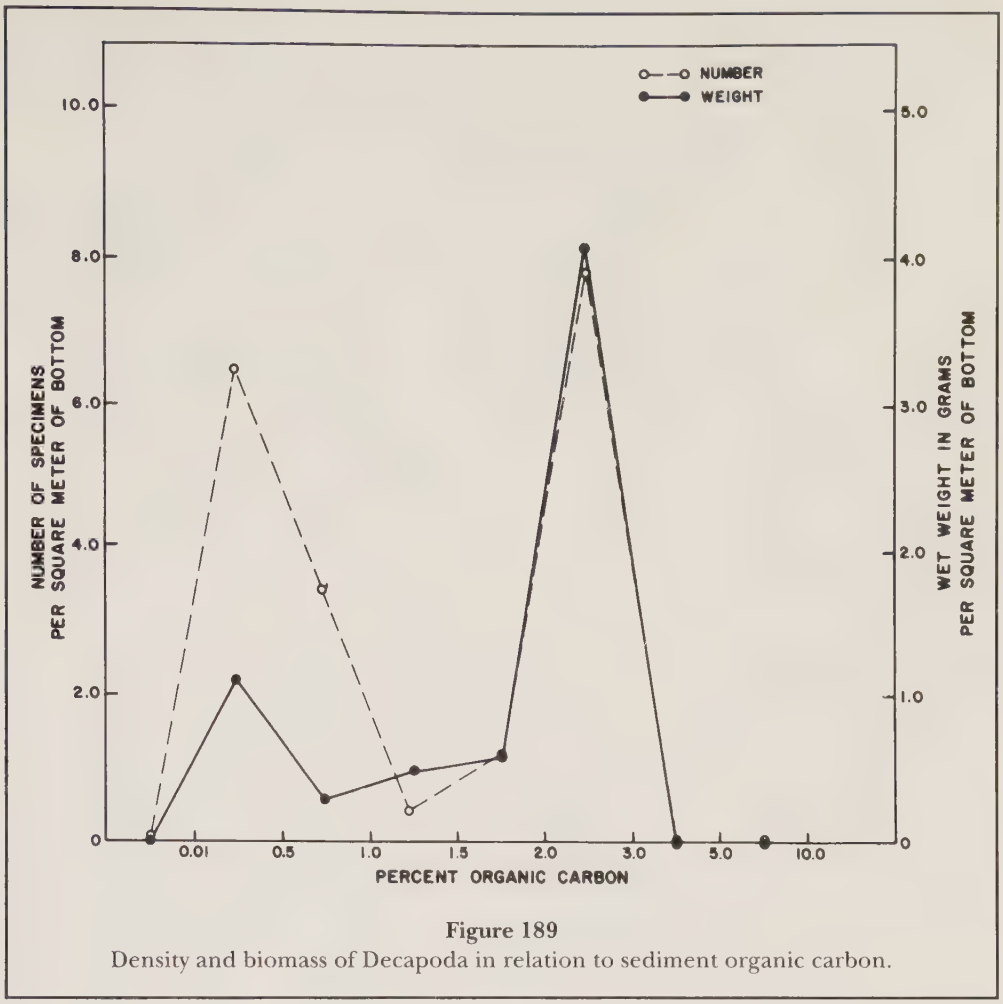


Figure 189
Density and biomass of Decapoda in relation to sediment organic carbon.

Geographic distribution

Bryozoans were distributed in somewhat scattered tracts in nearly all sections of the study area (Fig. 190). They occurred most commonly in coastal areas and on offshore banks. Specimens were noticeably scarce in the central part of the Gulf of Maine, over large portions of the eastern Nova Scotian Shelf, from offshore parts of the Southern New England Shelf, and on the continental slope and rise. Dense assemblages of over one hundred colonies per square meter were present in small areas dispersed throughout the banks and coastal areas.

In the six standard geographic areas, bryozoans were most prevalent, on the average, on Georges Bank (28 colonies/m^2) and on the Southern New England Shelf (22 colonies/m^2) (Table 6; Fig. 191). They were moderately common in the Nova Scotia and Gulf of Maine areas and scarce or absent in the two slope areas.

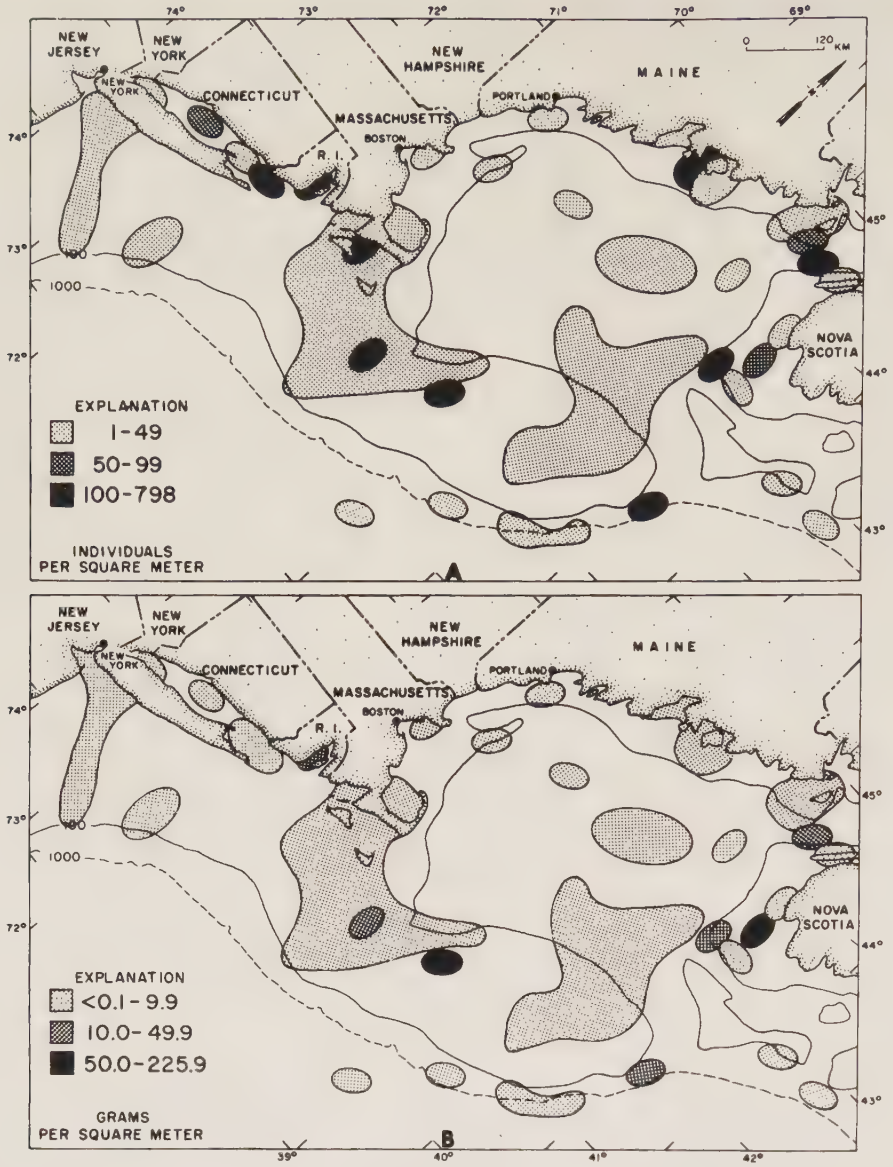
The largest average biomass, 6.3 g/m^2, occurred in the Nova Scotia area (Table 8; Fig. 191). Georges Bank ranked second with 2.6 g/m^2, and all other areas contained less than 1 g/m^2.

Incidence of occurrence in the four continental shelf areas generally diminished from a high of 19% in the northeast to a low of 11% in the southwest. Their occurrence was even lower, 6 and 0%, in the two slope areas (Table 10).

Bathymetric Distribution

Bryozoans were taken at water depths ranging from 8 to 3,820 m. There was a very pronounced decrease in the density as water depth increased (Table 11; Fig. 192). The average number of colonies in the shallowest (0–24 m) depth zone was 39/m^2 and decreased steadily to an average of 4.3/m^2 on the upper continental slope at a depth of 500 m. Below 500 m they were absent or present in very low (0.5 colony/m^2) quantities.

The average biomass of bryozoans was higher in shallow water than in deep water. This relationship was similar to that described above for density, except for an unusually large average biomass of 2.9 g/m^2 at depths between 50 and 99 m. This was the largest average biomass from any one depth class (Table 13; Fig. 192).



BRYOZOA

Figure 190

Geographic distribution of Bryozoa: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

The percentage of samples containing bryozoans generally decreased with increasing water depth. The highest incidence of occurrence (19%) was in the shallowest depth class. At depths greater than 500 m, they occurred in from 0 to 5% of the samples (Table 15).

Relation to Sediments

Bryozoans were especially common in the hard, coarse substrates that afforded suitable surfaces for attachment. In addition, they were also found in smaller quantities in the soft fine-grain sediments but attached to hard biogenic materials, occasional pieces of gravel, or man-made debris (Tables 16, 18; Fig. 193). Shell substrate seemed particularly suitable in as much as it yielded an average of over 300 colonies/m^2 and an average biomass of nearly 17 g/m^2. Moreover, bryozoans made up over 25% of the total number of specimens and 7.5% of the biomass of the total benthic fauna in shell substrates (Tables 17, 19). Gravel substrates ranked second in quantity, with an average density of 75 colonies/m^2 and a biomass of 7.4 g/m^2. Quantities were low (less than 6 colonies and 0.4 g/m^2) in the remaining four sediment types.

Incidence of occurrence was highest (50%) in shell, moderately high in till and gravel, and low (10% or less) in the fine-grain sediments (Table 20).

Relation to Water Temperature

Although bryozoans were rather severely limited in distribution by specific substrate requirements, water temperature range appeared to play a lesser role in inhibiting abundance. Members of this phylum occurred in all temperature range classes but revealed a pronounced trend of increasing density with a broadening of the temperature range (Table 21; Fig. 194). The density of bryozoans averaged only 3 colonies/m^2 where the temperature range was less than 4°C. Their density increased to an average of 66 colonies/m^2 where the temperature range was greater than 20°C.

Biomass values also exhibited a general upward trend (0.28–2.45 g/m^2) as the temperature range broadened. This increase, however, was less consistent than that exhibited by numerical density (Table 23; Fig. 194).

The occurrence of bryozoans in the samples ranged from 8 to 21%. Generally, incidence of occurrence was low where the temperature range was narrow, and high where the temperature range was broad (Table 25).

Relation to Sediment Organic Carbon

The relationship of bryozoans to sediment organic carbon was not nearly as well defined as that in other parameters because no orderly trend or pattern was discernible. Relatively high average densities, between 21 and 35 individual colonies/m^2, occurred in widely separated organic carbon content classes in the low, middle, and higher regions of the content spectrum (Table 26; Fig. 195). Significantly lower average densities, ranging between 0 and 8/m^2, occurred in adjacent carbon content classes, effectively separating and isolating the higher values.

Average biomass was distributed in a manner similar to that for density but was not as pronounced. Highest bryozoan biomasses (1.95 and 1.21 g/m^2) occurred in the low and upper middle carbon content range, interspersed with significantly lower values (Table 28; Fig. 195).

The percentage of samples containing bryozoans ranged from 0 to 25% (Table 30). Incidence of occurrence showed a general trend of decreasing (20 to 0%) as organic carbon content increased from 0 to 2.99%, but it shot up to 25% in the 3.00–4.99% class.

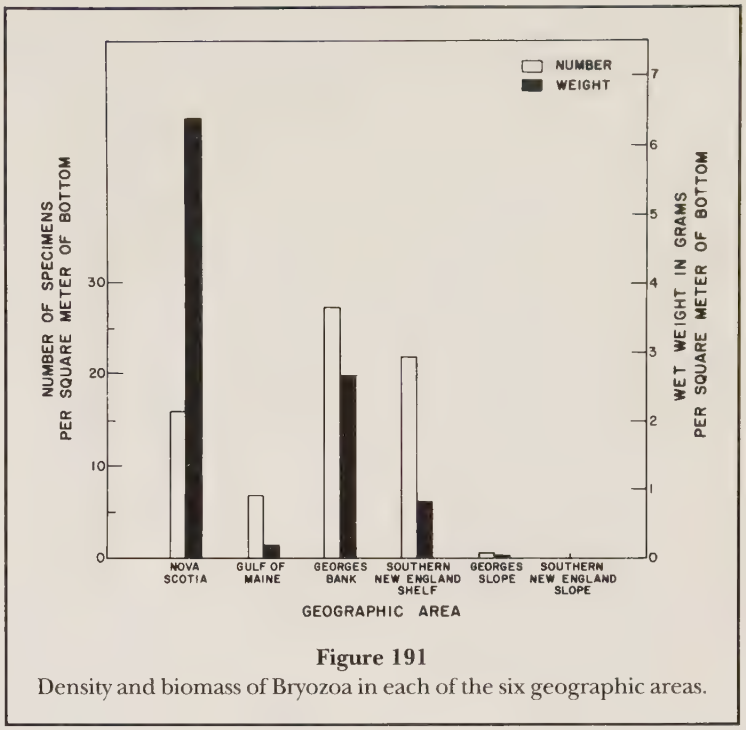


Figure 191
Density and biomass of Bryozoa in each of the six geographic areas.

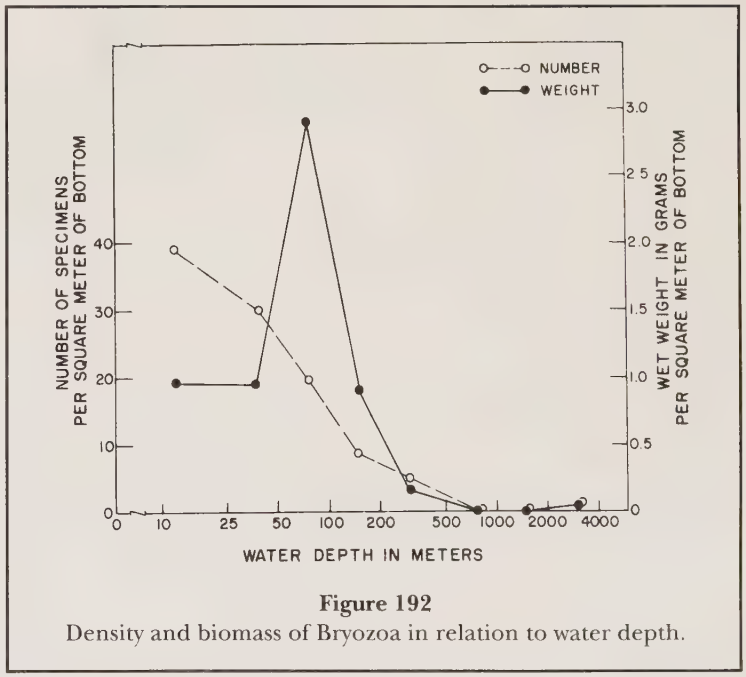


Figure 192
Density and biomass of Bryozoa in relation to water depth.

Brachiopoda

Brachiopods, commonly known as lamp shells, are sessile organisms normally found attached to rocks and other firm substrata at continental shelf depths, usually in cold water. These requirements limited the scope of their distribution to the northeastern sectors where suitable habitats were more prevalent than elsewhere in

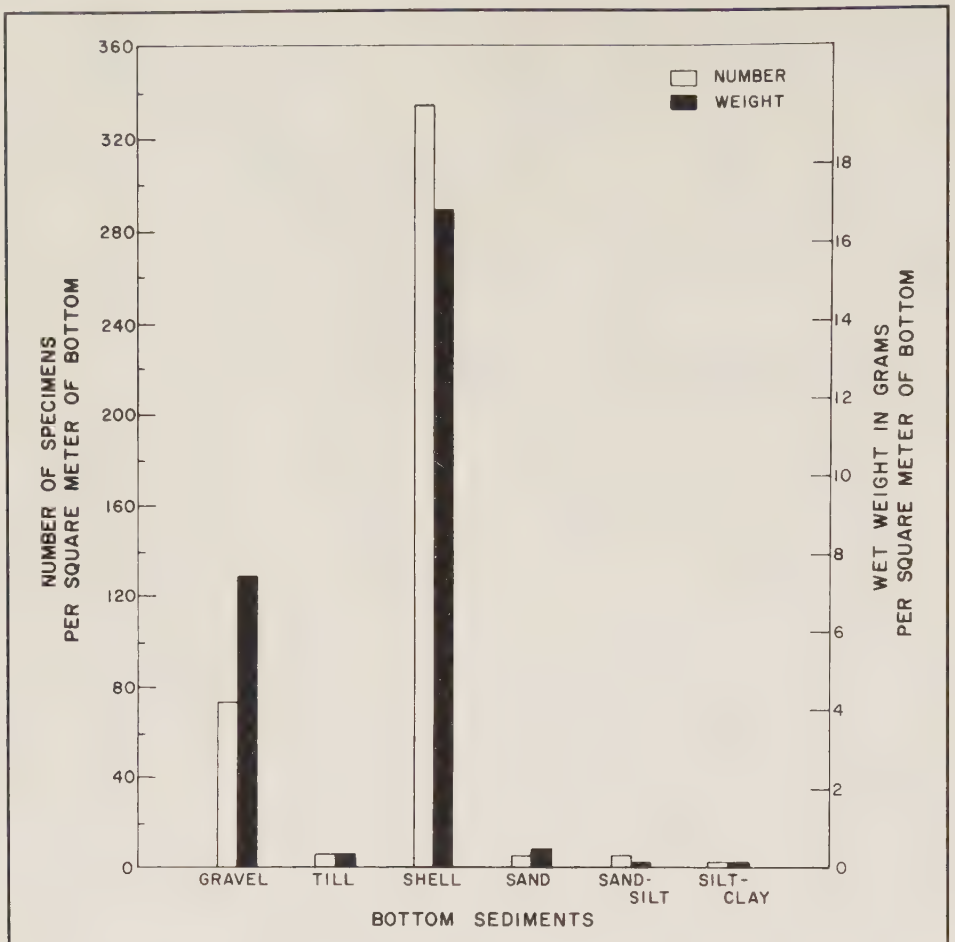


Figure 193
Density and biomass of Bryozoa in relation to bottom sediments.

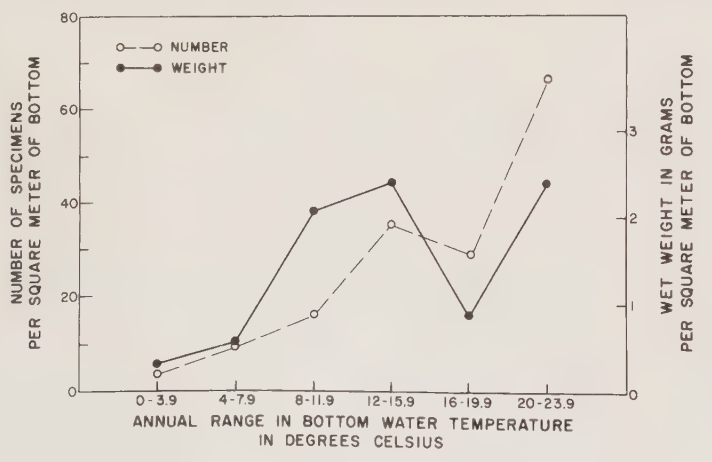


Figure 194
Density and biomass of Bryozoa in relation to the annual range of bottom water temperature.

the New England region. Although often locally significant in terms of density and biomass, their contribution to the total fauna was limited by the patchiness of suitable habitats. Brachiopods accounted for only 0.3% of the total number of specimens and 0.7% of the total biomass (Table 3).

Brachiopod diversity was also noteworthy. Although the phylum is not noted for large numbers of species, there being only about 280 known living species, our samples contained only members of one genus, *Terabratulina*.

Size of specimens ranged from about 5 mm to some large specimens of about 30 mm length. Color was typical for the genus with dull white and silvery gray hues predominating; many specimens were fouled by other sessile forms such as bryozoans, hydroids, and encrusting sponges of various hues, but tans, browns, yellows, and grays predominated.

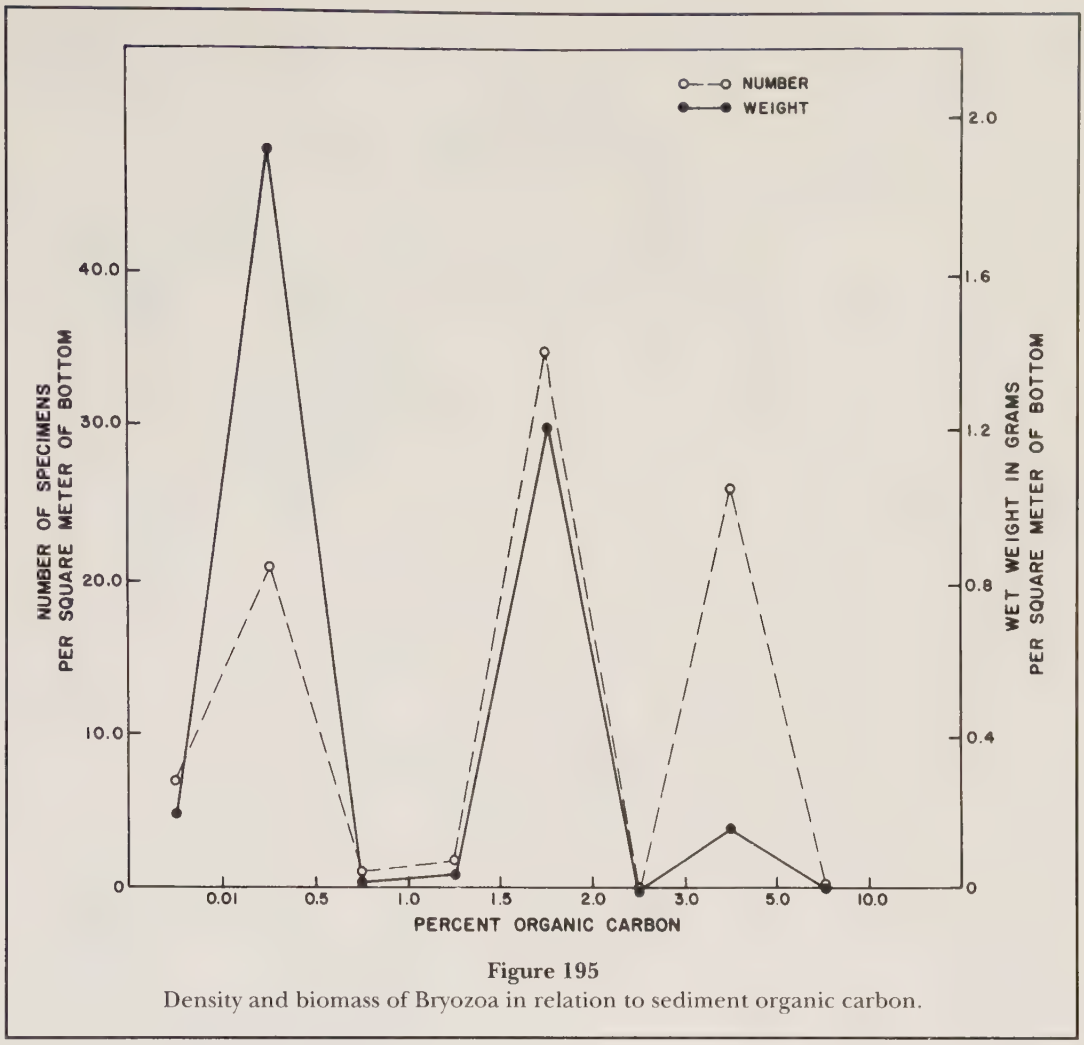


Figure 195
Density and biomass of Bryozoa in relation to sediment organic carbon.

Brachiopods occurred in 54 samples (5% of total). Their numerical density averaged 4.5 individuals/m^2, and their biomass averaged 0.89 g/m^2 (Table 5).

Geographic Distribution

Brachiopods were restricted to the northeastern sector of the study area, the only region in which suitable habitats were found (Fig. 196). Numerical density was usually low (<49 individuals/m^2) over most of their range as was biomass (<10 g/m^2); small areas of moderate (between 50 and 100/m^2) density and biomass (10 to 63 g/m^2) occurred in south-central Gulf of Maine adjacent to the northern edge of Georges Bank and on the Nova Scotian shelf. Significant densities (between 100 and 490/m^2) did occur in a few places, notably at the mouth of the Bay of Fundy.

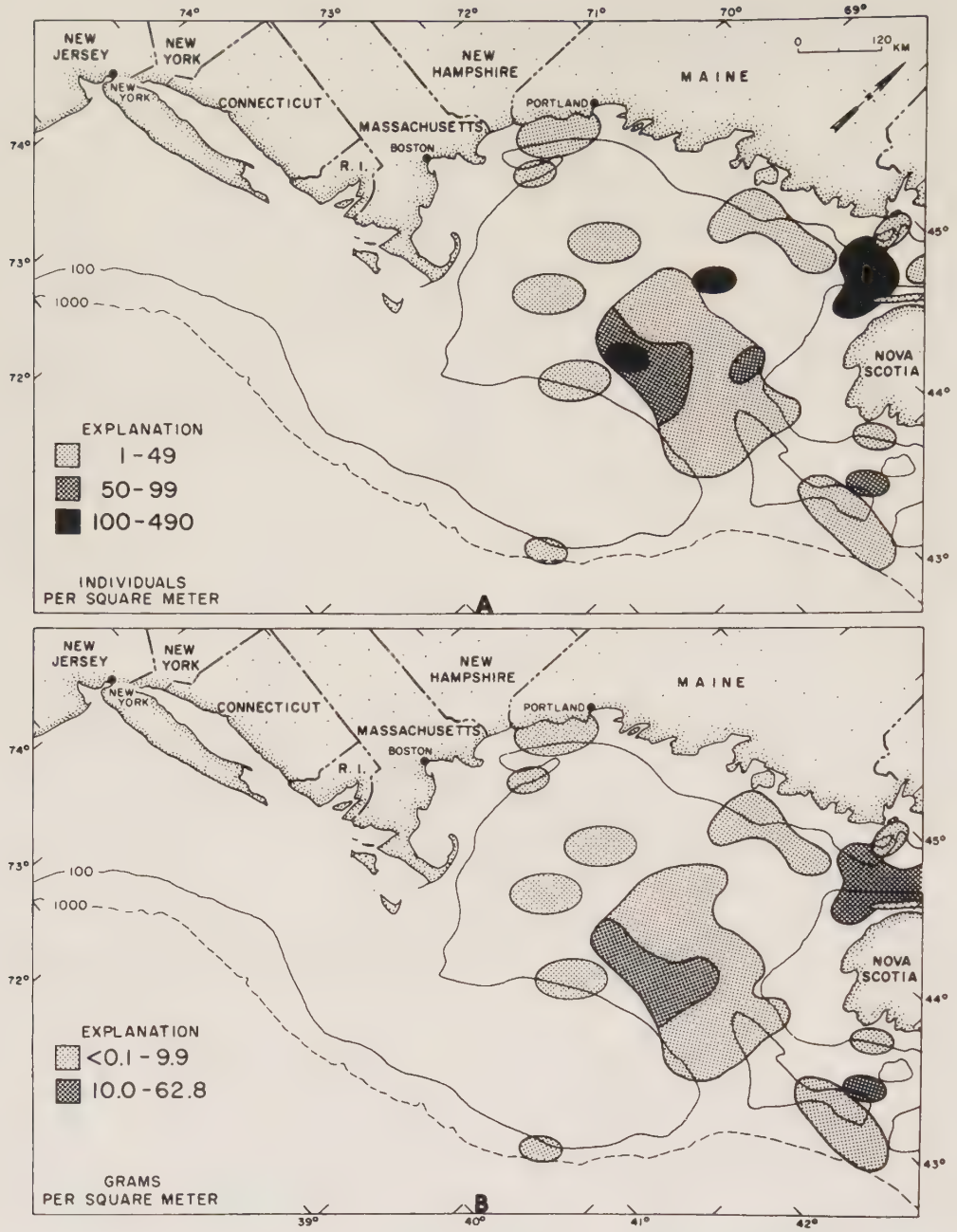
Among the six standard geographic areas brachiopods were restricted to Nova Scotia, the Gulf of Maine, and Georges Slope. Largest average density (22/m^2) and biomass (3.68 g/m^2) occurred off Nova Scotia followed by Gulf of Maine (9.5/m^2 and 2.12 g/m^2); Georges Slope contained insignificant quantities (Tables 6, 8; Fig. 197).

Twenty-one percent of the samples off Nova Scotia contained brachiopods versus 12% in the Gulf of Maine; only 2% of the Georges Slope samples yielded specimens (Table 10).

Bathymetric Distribution

Brachiopods were taken at depths between 51 and 690 m. Very few occurred in water deeper than 499 m (Tables 11, 13; Fig. 198). Largest average density and biomass were found at depths between 200 and 499 m in so-called upper slope depths; there density averaged 17 individual/m^2 and biomass nearly 4 g/m^2. Both average density and biomass decreased significantly with decreasing depth above 200 m.

Frequency of occurrence of brachiopods in the samples was moderate to low. The highest frequency was in the 200–499 m depth class at 14%; the rate



BRACHIOPODA

Figure 196

Geographic distribution of Brachiopoda: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

decreased to 5% in deeper water classes and to 10 to 2% in the shallower water depth classes (Table 15).

Relation to Sediments

Brachiopods occurred in all sediment types found in the region but showed a pronounced preference for the coarser types over the finer ones (Tables 16, 18; Fig. 199). Till sediments ranked first in preference, containing an average of 48 individuals/m^2 and an average biomass of nearly 16 g/m^2.

Interestingly, although shell sediments ranked second in terms of density (37/m^2), they ranked last (0.22 g/m^2) in terms of biomass. Gravel, with a mean density and biomass of 14/m^2 and 2.44 g/m^2, respectively,

ranked third. Both mean density (range 0 to 2/m^2) and mean biomass (range 0.24 to 0.33 g/m^2) were significantly lower in sand, sand-silt, and silt-clay, each of which offered very limited attachment potential.

Samples in till substrates yielded the highest occurrence frequency of specimens (41%), shell and gravel were about even, but considerably lower in overall frequency than till (17 and 14%, respectively; Table 20). Only 2 to 3% of samples in the other sediment types provided brachiopod specimens.

Relation to Water Temperature

Brachiopods were quite restricted in their relation to the annual range in water temperature and showed a very strong tendency of decreasing abundance with increasing temperature range (Tables 21, 23; Fig. 200). None were found where the annual temperature range exceeded 11.9°C. They were most plentiful (average density of 9/m^2 and biomass of 1.93 g/m^2) in the narrowest (0–3.9°C) temperature range and declined rapidly and steadily as the temperature range broadened.

The frequency of occurrence of brachiopods in samples in the temperature range groupings was low (10 to 2%) and followed the trend established in the abundance measures (Table 25).

Relation to Sediment Organic Carbon

Brachiopods preferred low levels of sediment organic carbon (Tables 26, 28; Fig. 201), being absent at levels above 1.49% carbon content. Numerical density was 3 to 5 times (range 16 to 3/m^2) higher where no measurable carbon was found than where small amounts occurred. Biomass was greatest (1.74 g/m^2) in the 0.5 to 0.99% carbon content class versus a slightly lower biomass (1.31 g/m^2) in the 0% grouping. Significantly lower levels occurred in the other carbon content groupings.

Frequency of occurrence of brachiopods in samples declined rapidly from a high of 40% in the 0% organic carbon level grouping to only 6% in the next (0.01–0.49%) grouping, then more slowly to 2% in the 1.00 to 1.49% grouping (Table 30).

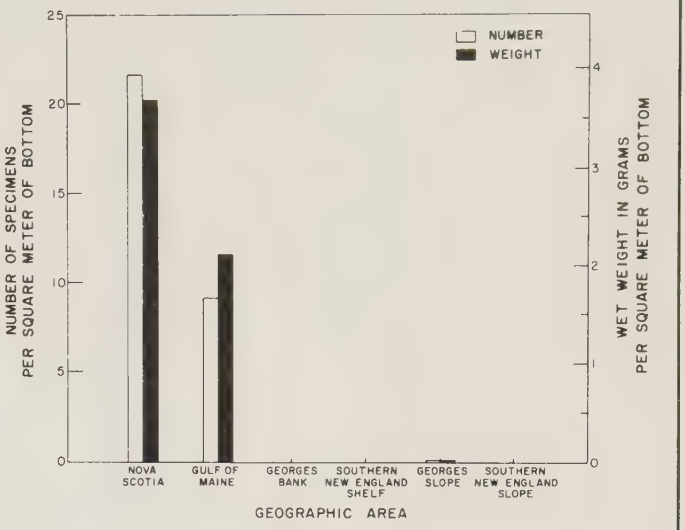


Figure 197

Density and biomass of Brachiopoda in each of the six geographic areas.

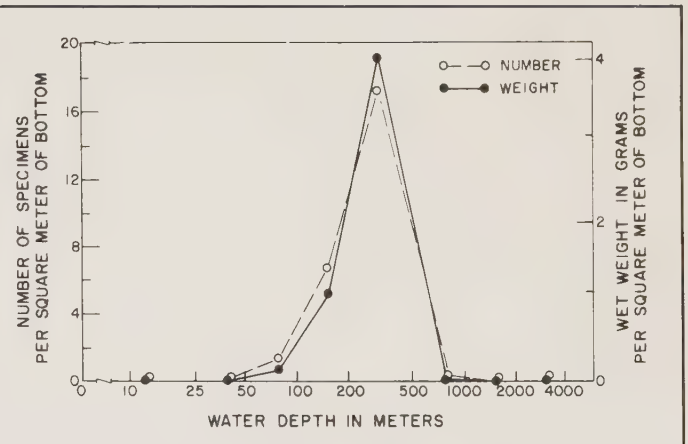


Figure 198

Density and biomass of Brachiopoda in relation to water depth.

Echinodermata

The phylum Echinodermata is represented, in the New England region, by members of five classes: Crinoidea, Holothuroidea, Echinoidea, Ophiuroidea, and Asteroidea. All but Crinoidea provide significant contributions to the total benthic fauna. In terms of contribution to overall density, members of Echinoidea are second in dominance, providing 20% of the total number of organisms in the region, and Holothuroidea rank fourth with a 7% contribution (see Table 3). Ophiuroidea and Asteroidea are subdominants, providing 1.8 and 1.2%, respectively, of the total number of organisms. In terms of biomass, however, none of the four rank among the top dominants, but Ophiuroidea and Echinoidea are subdominants providing 2.9 and 1.9%, respectively, of the total. Holothuroidea and Asteroidea contributions to biomass, 0.3 and 0.1% respectively, are significantly below their showing in terms of density (see Table 3).

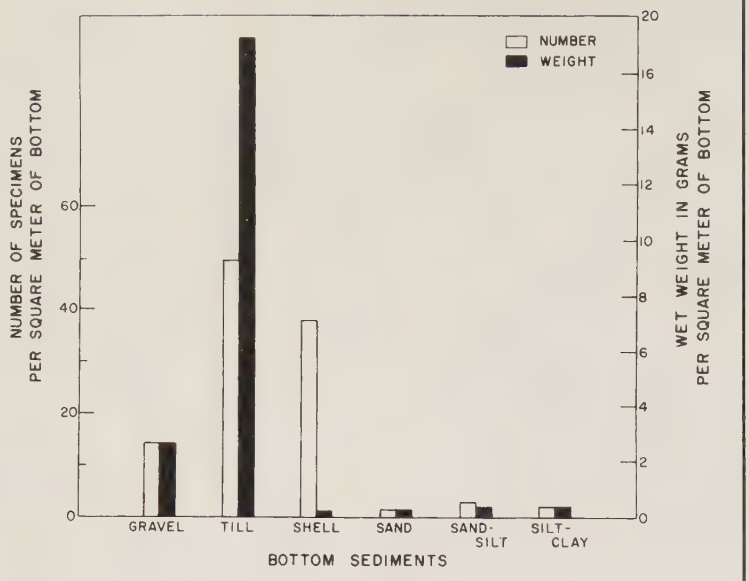


Figure 199
Density and biomass of Brachiopoda in relation to bottom sediments.

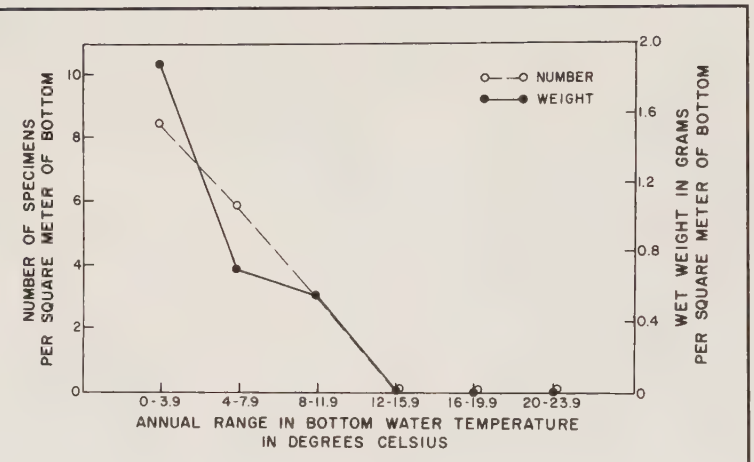


Figure 200
Density and biomass of Brachiopoda in relation to the annual range of bottom water tempereature.

Following the procedure established above for the other major taxa, the figures relating to Echinodermata (Figs. 202–207) will be presented here, and a detailed discussion of the phylum will be presented in the section "Dominant Components of the Macrobenthos" below. Discussion of the five classes of echinoderms follows.

Crinoidea—Crinoids formed a minute portion of the New England benthic fauna. Members of this group were obtained at only two stations. Six specimens that totaled 0.16 g in weight were taken at station 1038 in the Gulf of Maine. Water depth at this locality was 203 m; bottom sediments were of sand-silt. Two specimens that weighed 0.02 g were taken at station 2185 in the Georges Slope area. Water depth at this locality was 1,420 m; bottom sediments were composed of silt-clay. The annual range in bottom water temperature at each of these sites was less than 4°C. Organic carbon content at station 1038 was 0.40% and at station 2185, 0.55%.

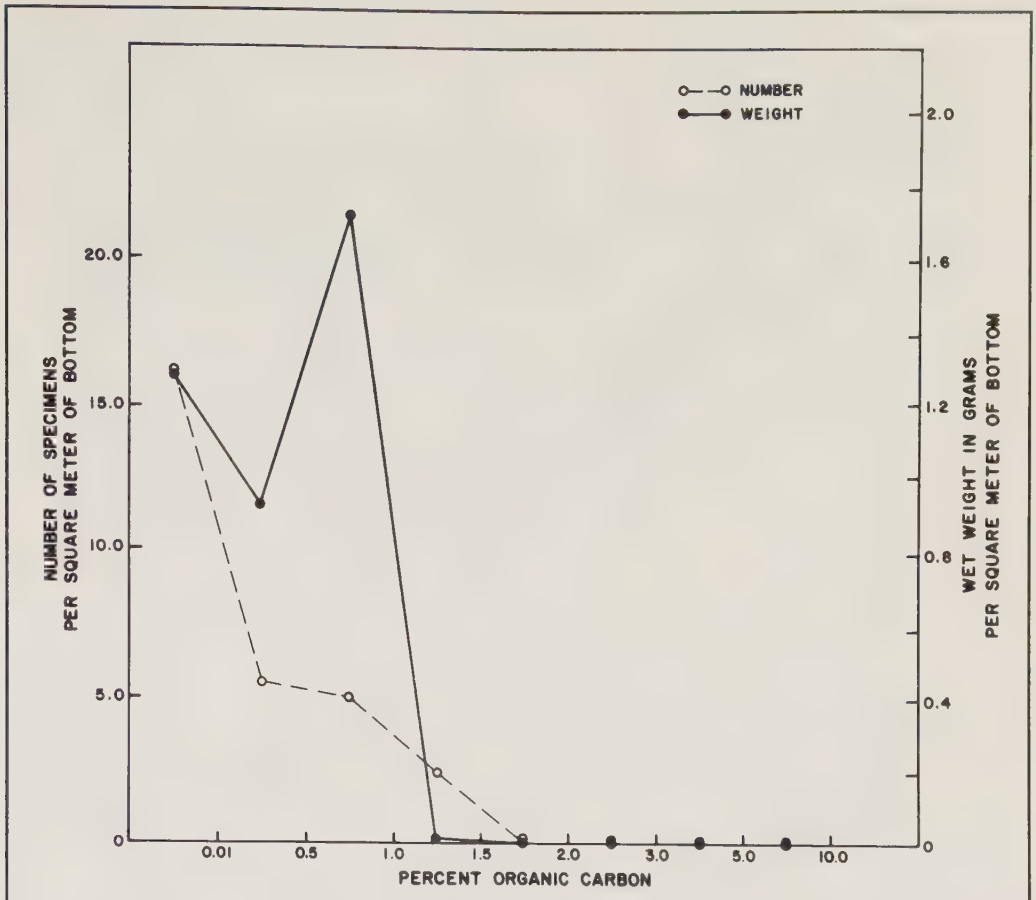


Figure 201
Density and biomass of Brachiopoda in relation to sediment organic carbon.

Holothuroidea—Holothurians formed a moderate component of the New England benthos in terms of biomass, but made up only a minor portion of the total number of specimens (Table 3). This was due mainly to the relatively large size of individual specimens. Members of this group averaged 3 g each, which is a size unsurpassed by any other major faunal group collected in this study. The larger specimens, *Cucumaria* and *Molpadia,* were 10 to 14 cm long, and 2 to 4 cm in diameter. The smallest specimens were juvenile *Psolus* about 4 mm in length.

Five orders of holothurians were represented in the samples (Table 4). The dominant group, from the standpoint of abundance and taxonomic diversity, was the Dendrochirotida. Few species and specimens were taken belonging to the orders Molpadiida, Apodida, Aspidochirotida, and Dactylochirotida.

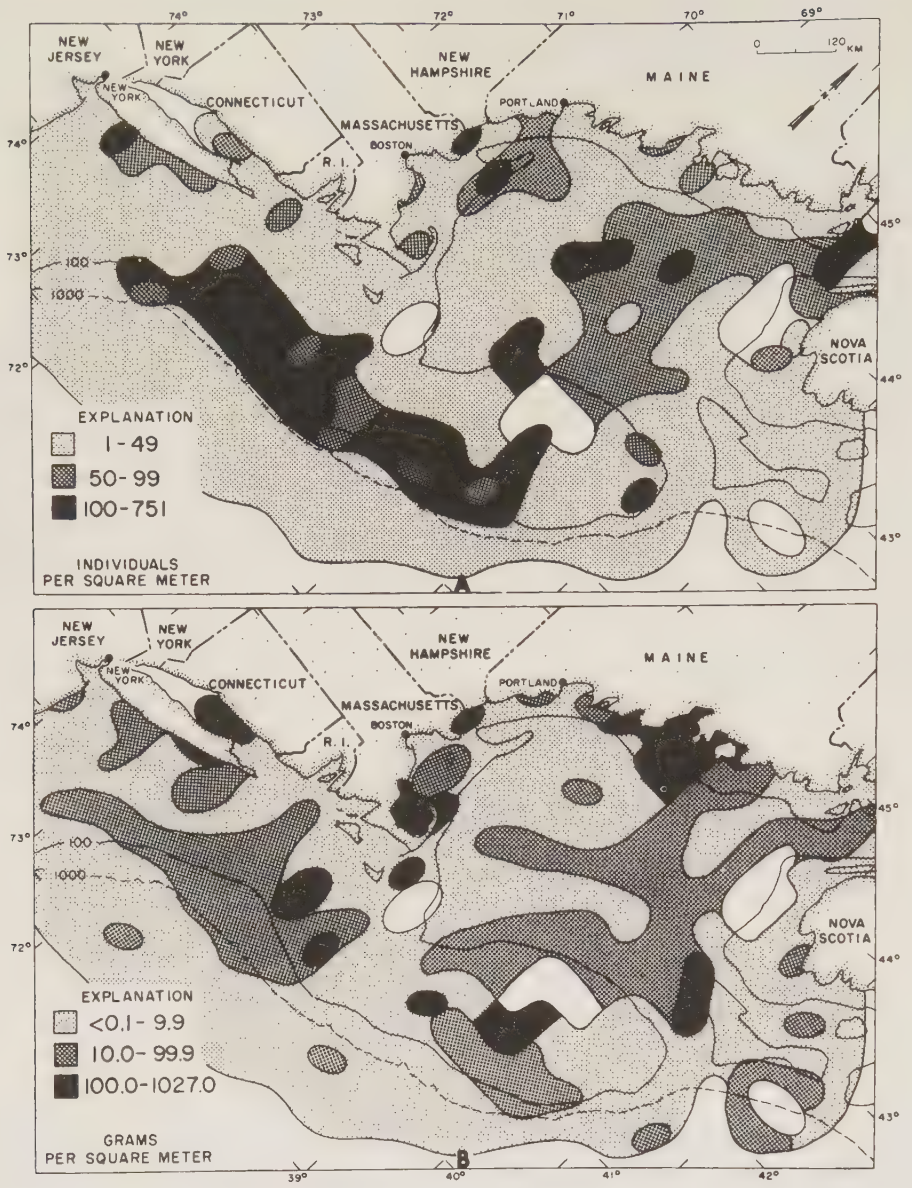
Color of specimens in this region was generally uniform over the body surface (except for the contrasting light colored tube feet in some species), which usually was reddish-brown, tan, or occasionally light cream. One small species was very dark violet and black.

Holothurians occurred in 202 samples (19% of total). Their density averaged 4.3/m^2 and their biomass averaged 12.9 g/m^2 (Table 5).

Geographic Distribution

Holothurians were prevalent over large sections of the Gulf of Maine and in the offshore Southern New England Shelf area (Fig. 208). They occurred on Georges Bank in low densities and in very few samples. Relatively high densities (25 to 88 individuals/m^2) occurred over rather large portions of the central Gulf of Maine and along the southern end of Great South Channel. In most localities, however, the average densities were less than 9 dividuals/m^2. In terms of biomass, holothurians were present in substantial quantities, usually greater than 1 g/m^2, and not uncommonly in quantities of 10 to over 50 g/m^2.

Among the six standard geographic areas, holothurians were present in largest quantities in the Gulf of



ECHINODERMATA

Figure 202

Geographic distribution of Echinodermata: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

Maine area (Tables 6, 8; Fig. 209), where the average density was nearly 8 individuals per/m^2 and the biomass averaged more than 27 g/m^2. The Georges Bank area had the lowest average density, 0.2/m^2, and an average biomass of only 0.5 g/m^2. The other four areas had intermediate quantities.

Holothurians accounted for a small proportion of the total number of specimens in all areas, but made up a substantial part of the total weight in two areas (Table 9). In the Gulf of Maine area they accounted for 22% of the total faunal weight and on the Southern New England Slope they made up 14% of the total faunal weight.

The occurrence of holothurians in the samples was moderately low (17 to 40%) in all areas except Georges Bank, where they were present in only 2% of the samples. They were present in a slightly higher proportion of the samples from the two slope areas than from the shelf areas (Table 10).

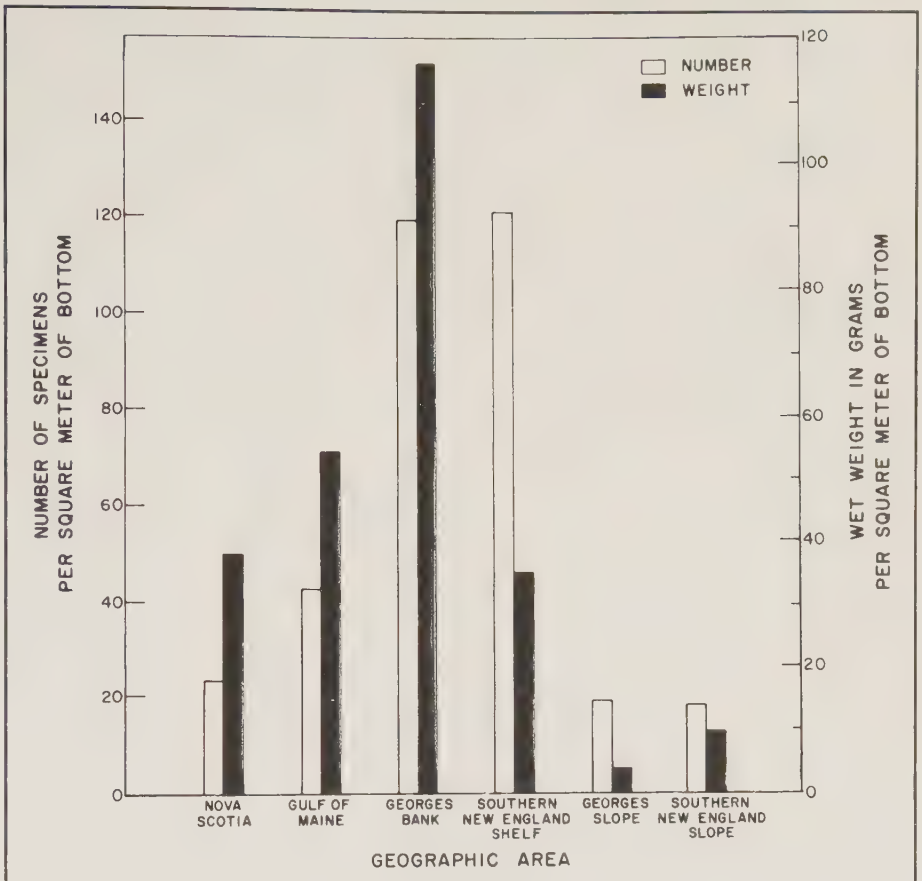


Figure 203
Density and biomass of Echinodermata in each of the six geographic areas.

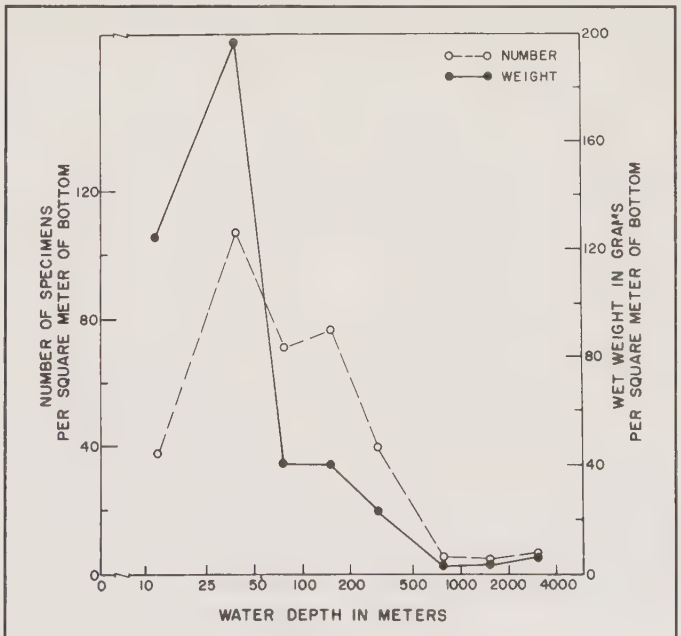


Figure 204
Density and bomass of Echinodermata in relation to water depth.

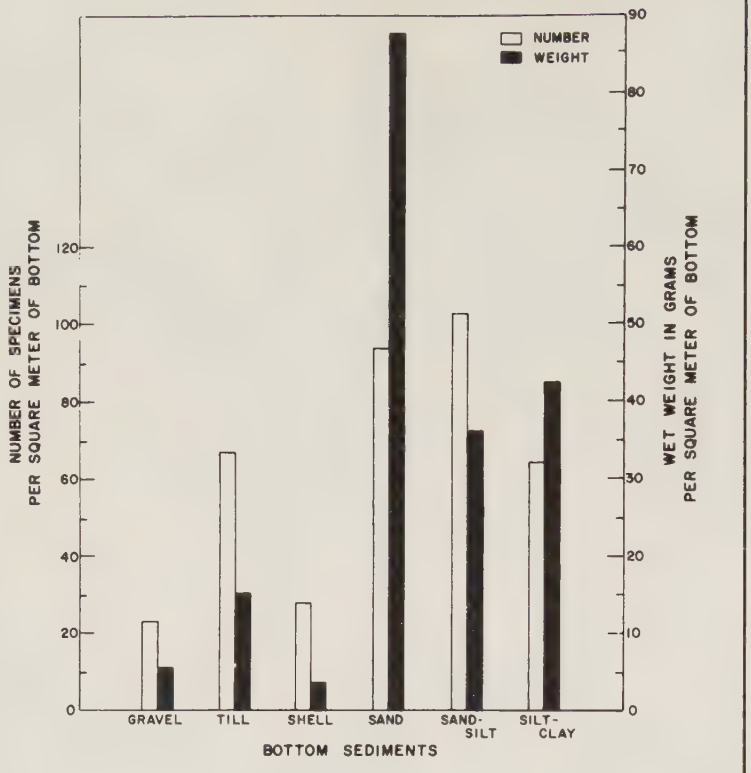


Figure 205
Density and biomass of Echinodermata in relation to bottom sediments.

Bathymetric Distribution

Holothurians were collected at depths ranging from 6 to 3,820 m, and were present in all depth classes over this broad depth range (Table 11; Fig. 210). Densities were highest (average 4 to 10 individuals/m^2) at intermediate depths (50 to 500 m) and somewhat lower (0.7 to 1.9/m^2) in both shallower and deeper bathymetric classes.

Biomass distribution of holothurians differed substantially from the depth-density relationship (Table 13; Fig. 210). Highest biomass averages (13 to 37 g/m^2) were found in depths less than 100 m. Lowest biomass (0.2 g/m^2) occurred at 500 to 999 m; intermediate quantities (1 to 6 g/m^2) were found in other depth classes.

Individual holothurians from shallow water (0 to 24 m) were larger, averaging nearly 25 g each, and size decreased with increasing depth to less than 1 g each at depths greater than 500 m.

The frequency of holothurian occurrence was higher in samples from deep water than in those from shallow water (Table 15). At depths less than 50 m they were present in 8 to 9% of the samples, whereas, in water depths greater than 50 m they occurred in 14 to 33% of the samples.

Relation to Sediments

Holothurians were relatively numerous in till substrates and much less common in all other bottom types (Table 16; Fig. 211). Their average density in till was 25 individuals/m^2, whereas, in the other types of sediments their density was only 2.0 to 7.4/m^2.

The relationships of holothurian biomass to sediments were entirely different from those pertaining to density. The biomass was high (25 to 29 g/m^2) in sand-silt and silt-clay (Table 18; Fig. 211). In fact, holothurians accounted for from 15 to over 33%, respectively, of the total benthic biomass in those two sediment types (Table 19). In other types of sediments their biomass was moderate to small (4.7 to 0.4 g/m^2).

The presence of relatively fewer but larger specimens in soft sediments and numerous small specimens in till sediments accounts for the disparity between the biomass and density values in these substrates. In the other sediment types they were generally more equally distributed in density and biomass.

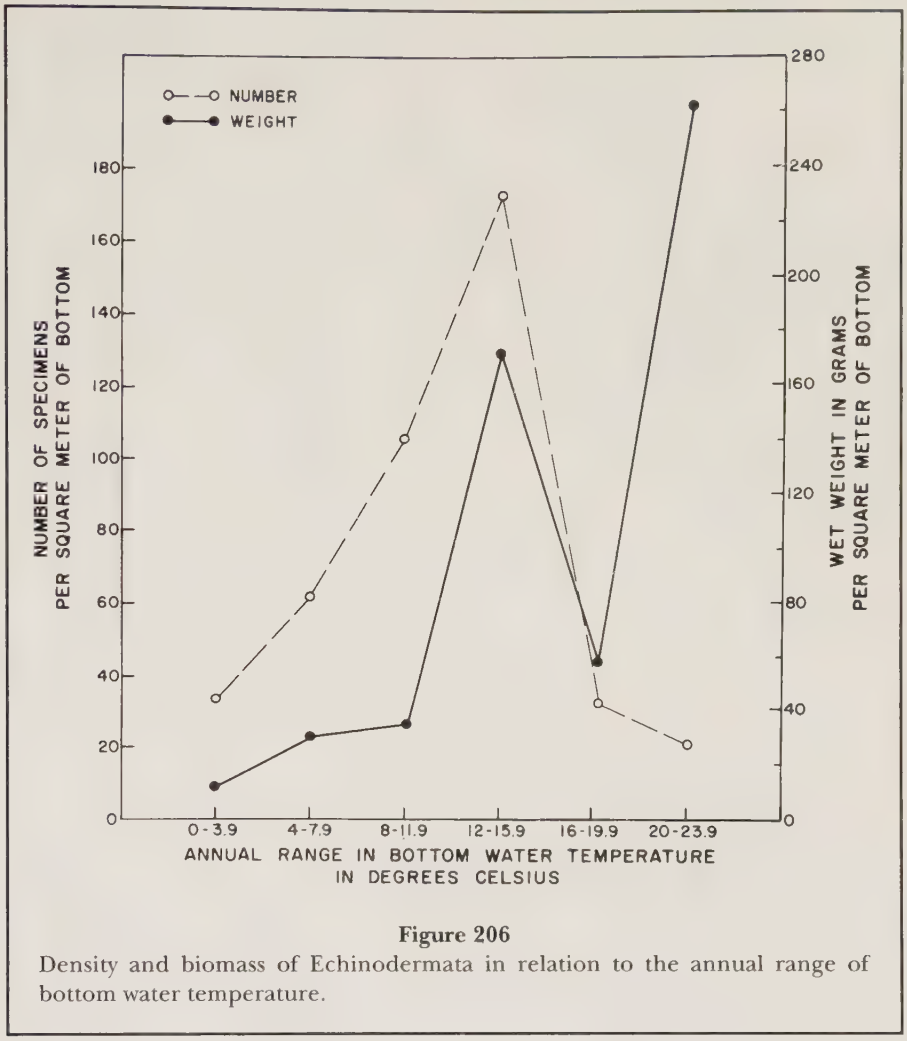


Figure 206
Density and biomass of Echinodermata in relation to the annual range of bottom water temperature.

Frequency of occurrence was moderate to low in all sediment types, and the relationship of holothurians with various sediments was similar to that described for numerical density (Table 20). Occurrence was highest (50%) in till, lowest (8%) in sand, and intermediate (16 to 36%) in the other sediment types.

Relation to Water Temperature

The relation of holothurian numerical density to the range in water temperature was the opposite of that exhibited by their biomass. Density generally decreased as the temperature range increased (Table 21; Fig. 212). The average density of holothurians was about 6 individuals/m^2 where the temperature range was less than 4°C and decreased to about 2 individuals/m^2 where the temperature variation was 16° to 19°C.

Conversely, the biomass of holothurians increased as water temperature ranges increased (Table 23; Fig. 212). Their biomass was relatively small (3 g/m^2) where the temperature range was small (<4°C). With increased annual temperature range, the biomass of holothurians increased substantially to an average of 128 g/m^2 where the range was greatest (20°–23.9°C).

Size disparity of specimens in the various temperature range classes was the principal cause of the reversed trends. The size of specimens increased markedly in waters having a broad temperature range, whereas the numerical density diminished slightly.

Holothurians contributed a moderately large proportion (4–9%) of the total biomass in five of the six temperature range classes. In the other class, where the temperature variation was high (>20°C), they contributed an extraordinarily large share (>30%) of the biomass (Table 24).

Frequency of occurrence was quite uniform at a moderate level (14–25%) in all temperature range classes except one (16°–19.9°C), in which holothurians contributed only 8% of the samples (Table 25).

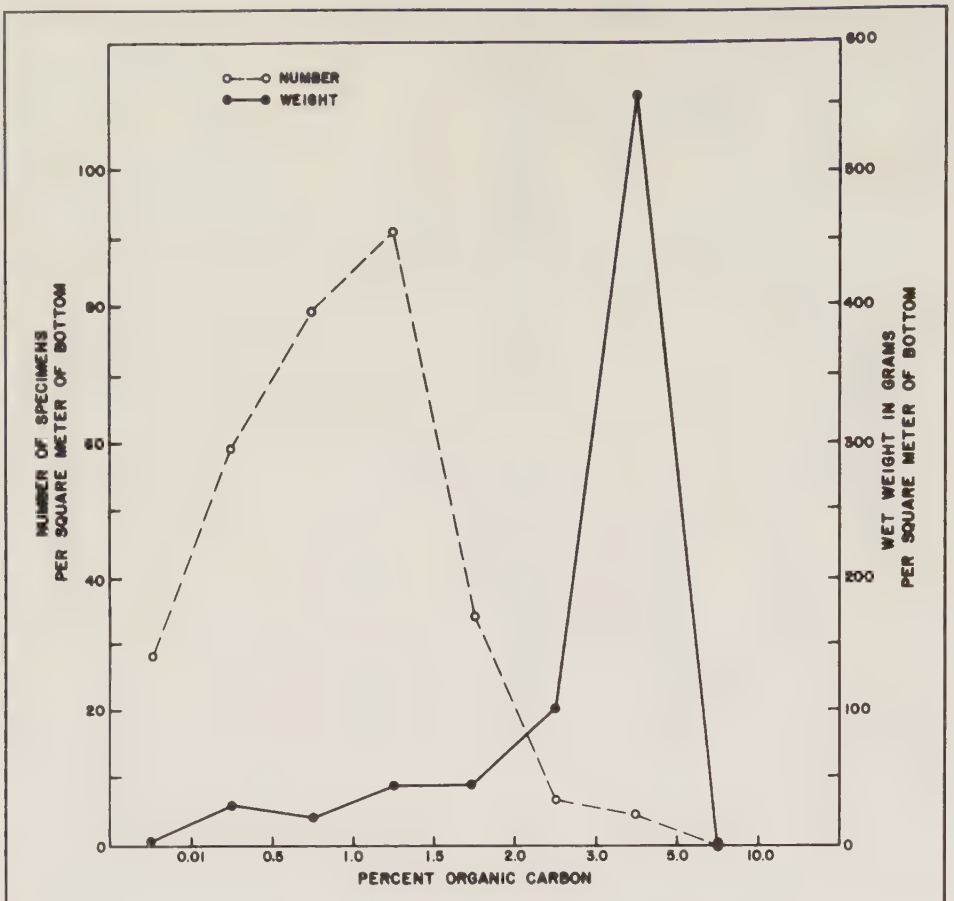


Figure 207
Density and biomass of Echinodermata in relation to sediment organic carbon.

Relation to Sediment Organic Carbon

Holothuroidea was one of only a very few taxonomic groups for which definite, consistent trends were clearly demonstrated in relation to the amount of organic carbon in the sediments.

The trend was the reverse of that pertaining to water temperature. The organic carbon-density relationship was in general negatively correlated, whereas the organic carbon-biomass relationship was essentially positively correlated. Seven of the eight carbon content classes were occupied; the one exception was the highest class (5.0+%).

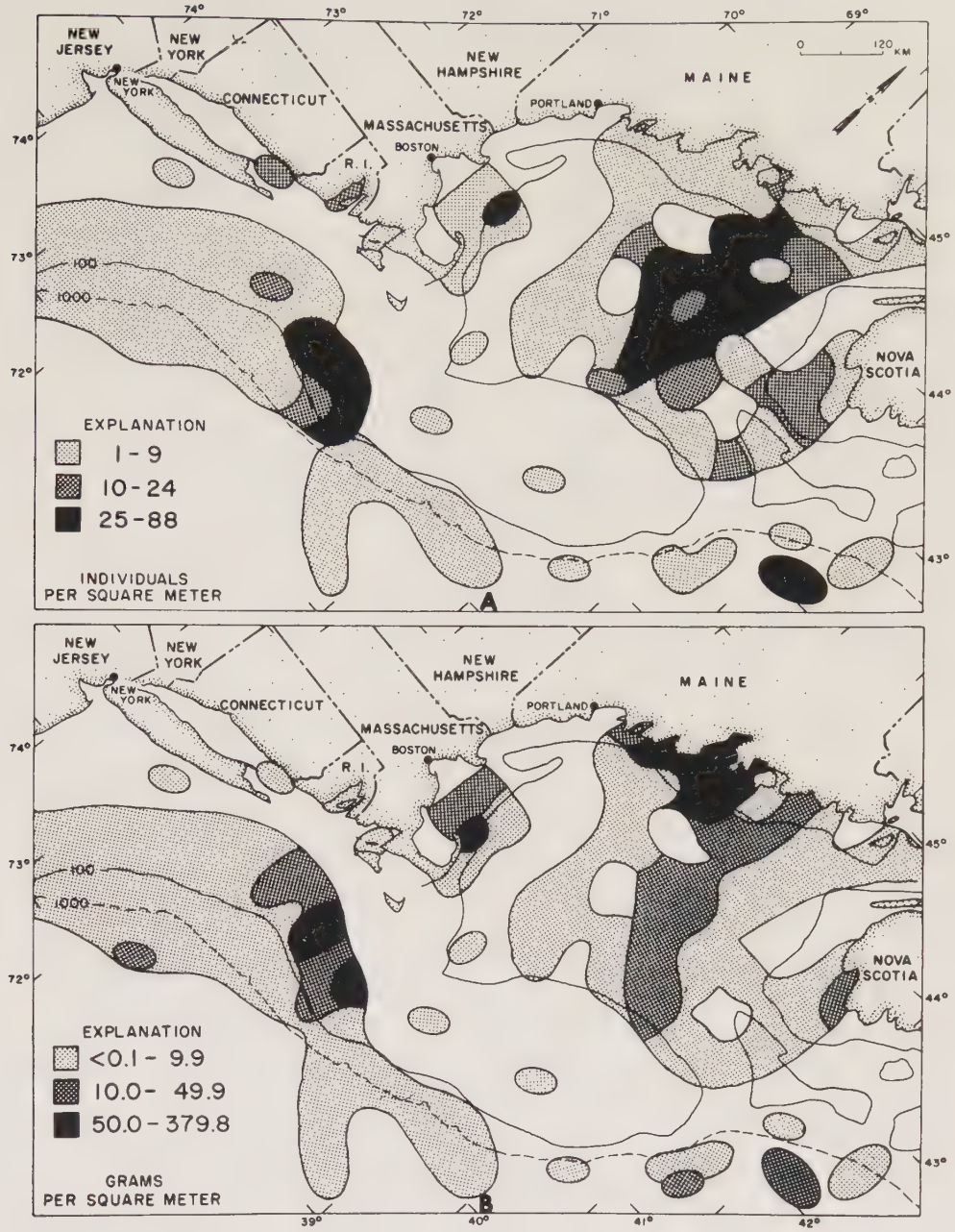
Holothurian average density was highest (18 individuals/m^2) where no measurable organic carbon was found (Table 26; Fig. 213). Much lower average densities (ranging from 8 to 2/m^2) prevailed in the other carbon content classes with a general tendency of decreasing with increasing organic carbon content.

Average biomass, on the other hand, showed a trend that was the reverse of the one for density (Table 28; Fig. 213). Average biomass was lowest (6 g/m^2) in the 0% carbon content class and steadily increased with increasing organic carbon content, culminating in exceptionally large biomasses in the two highest classes occupied. There was nearly a threefold increase between the 1.50 and 1.99% class and the 2.00 and 2.99% class (41 vs. 104 g/m^2) and a fivefold increase from the latter class to the 3.00–4.99% class (562 g/m^2).

Frequency of occurrence was quite uniform at a moderate level (15 to 40%) in all organic carbon content classes (Table 30).

Echinoidea—Sea urchins are the second largest (after bivalves) contributors to the New England benthic biomass, providing 20% of the total (Table 3). This large contribution was made by a group with low taxonomic diversity. Fewer than six species contributed over 95% of the specimens. The major contributors were sea urchins, heart urchins, and sand dollars.

The feeding habits of echinoids are varied. Most are bottom feeders (carnivores, herbivores, or omnivores), but some common species are plankton feeders, and



HOLOTHUROIDEA

Figure 208

Geographic distribution of Holothuroidea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

the distinction is not always maintained. When the preferred food types are unavailable, echinoids may may revert to other food sources, or in some species, to a different mode of feeding.

Echinoids in turn are preyed upon by a variety of benthic and nektonic animals. They have been observed in the diet of crabs, starfish, finfish, lobsters, birds, and mammals, including man. The quantity utilized for human consumption in recent years has increased with an annual harvest worth several million dollars.

Coloration of most of our echinoids was rather drab consisting largely of grays, brown, reddish-browns, and brownish-violet. In many species the color was gray or brown with suffusions of white, green, pink, or violet.

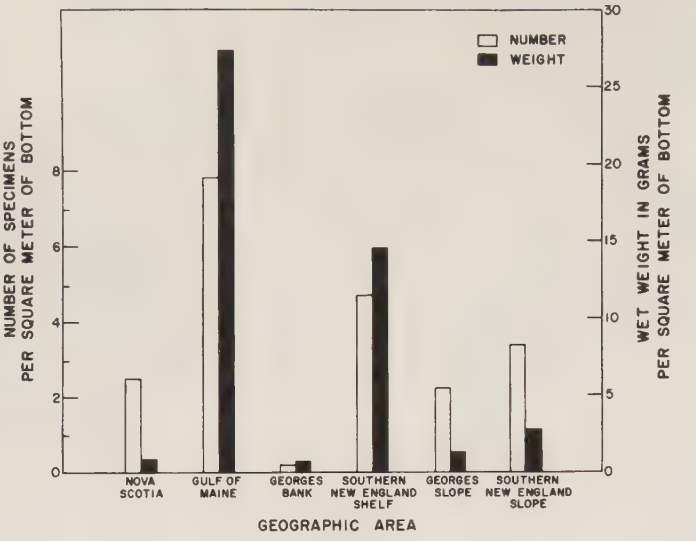


Figure 209
Density and biomass of Holothuroidea in each of the six geographic areas.

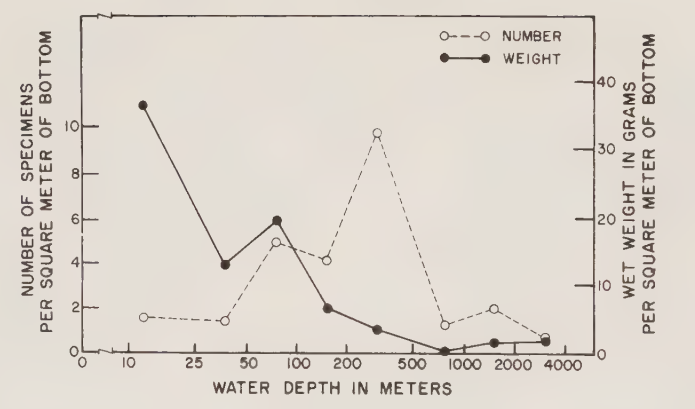


Figure 210
Density and biomass of Holothuroidea in relation to water depth.

Sizes ranged from 2 mm in diameter, in juvenile specimens, to large adults having a test diameter of 5 cm. The majority of specimens ranged between 0.5 and 3 cm.

Echinoids occurred in 293 samples (27% of the total). Their density averaged 29.3/m^2 and their biomass averaged 36.8 g/m^2 (Table 5).

Geographic Distribution

Echinoids occurred extensively throughout most of the study area (Fig. 214), but their distribution pattern was somewhat patchy and irregular in density. Intermediate and high densities (10 to 1,051 individuals/m^2) were common from Georges Bank to the Southern New England Shelf areas. The biomass of echinoids was especially high (100 to 1,027 g/m^2) on Georges Bank where they made up 50% of the total benthic biomass in Northeast Channel, and in coastal areas of central and Southern New England (24%).

Among the six standard geographic areas, the average density of echinoids was moderately high (over 100 individuals/m^2) on Georges Bank, intermediate (4 to 22/m^2) in the Nova Scotia, Gulf of Maine, and Southern New England Shelf areas; and low (0.2 and 0.3/m^2) in the two slope areas (Table 6; Fig. 215).

Biomass was moderate to very high in all areas. It was especially high (averaging 117 g/m^2) in the Georges

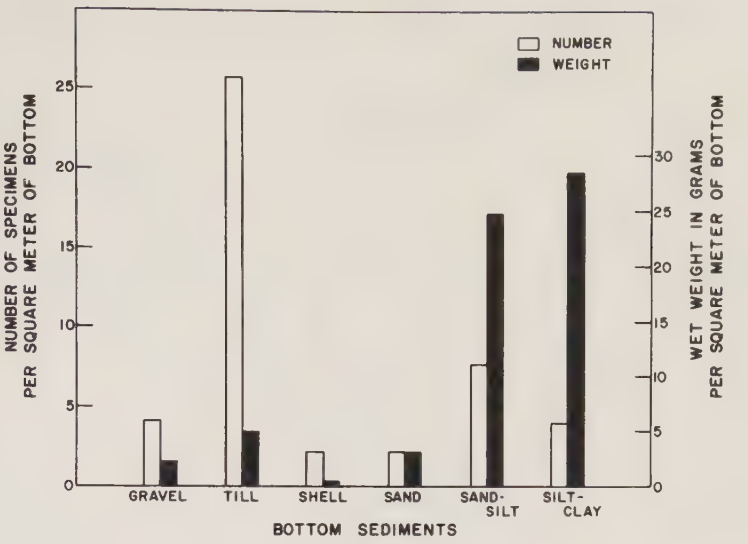


Figure 211
Density and biomass of Holothuroidea in relation to bottom sediments.

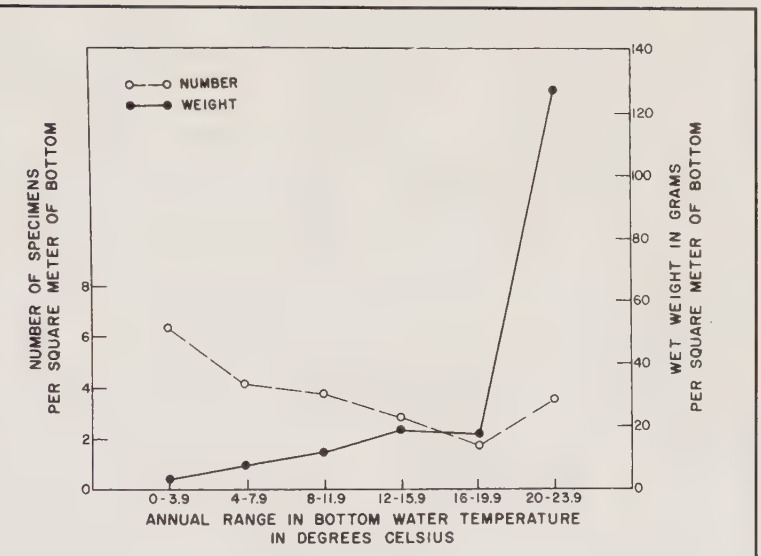


Figure 212
Density and biomass of Holothuroidea in relation to annual range of bottom water temperature.

Bank area. Moderately high (13 to 33 g/m^2) biomasses of echinoids were found off Nova Scotia, in the Gulf of Maine, and on the Southern New England Shelf. Lowest biomass averages occurred in the slope areas (Table 8; Fig. 215).

Echinoids were present in only moderate to small percentages of the total number of samples. Frequency of occurrence was moderate (19 to 51%) in the four continental shelf areas, and low (8 to 9%) in the two slope areas (Table 10).

Bathymetric Distribution

Echinoids occurred in water depths ranging from 7 to 2,950 m. Average densities were highest (127 individuals/m^2) near mid-shelf depths (25 to 49 m) and diminished in both shallower and deeper regions (Table 11;

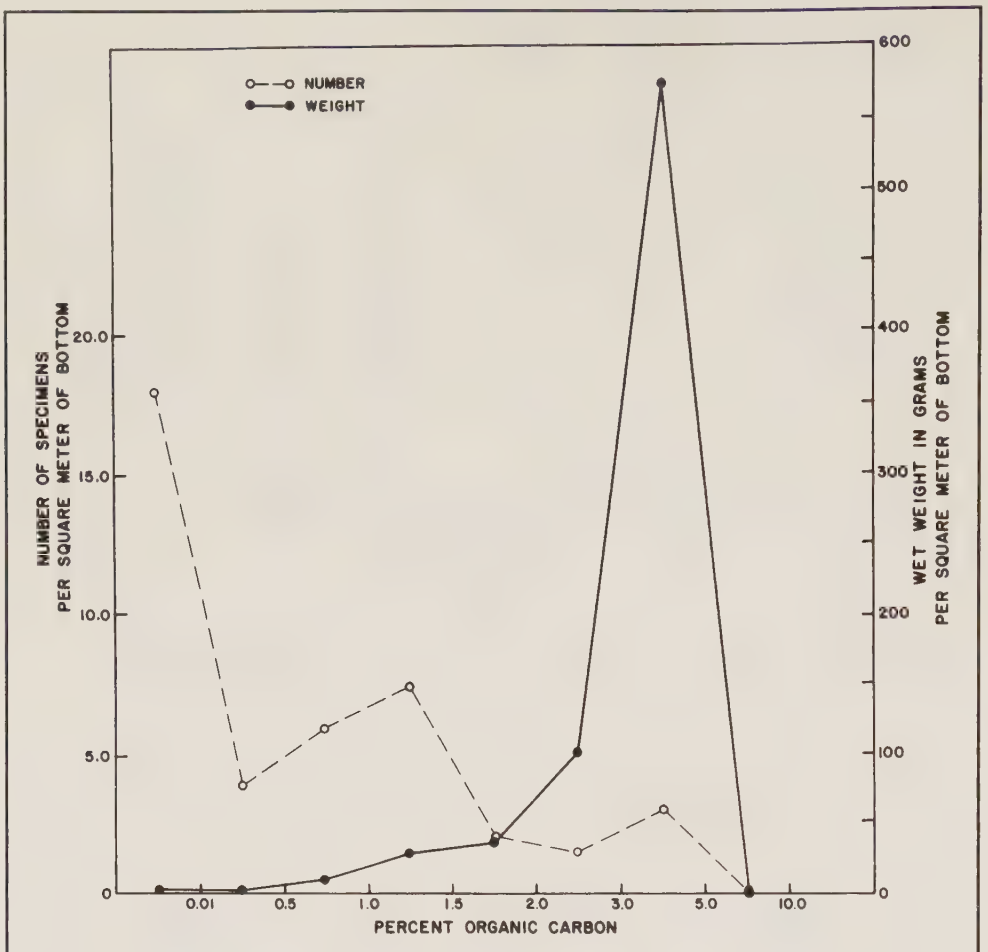


Figure 213
Density and biomass of Holothuroidea in relation to sediment organic carbon.

Fig. 216). At depths greater than 100 m, their density was drastically reduced (2.0 or fewer individuals/m^2).

The pattern of biomass distribution was quite similar to that for density. Average biomass was exceptionally high (154 g/m^2) near mid-shelf depths (25 to 49 m) and decreased in both shallower and deeper regions (Table 13; Fig. 216). The decrease was only moderate in the shallower depth class but was severe (0 to 1.8 g/m^2) in depths greater than 500 m.

Occurrence of echinoids in the samples was moderate to low in all depth classes and followed the same trend as density and biomass. They were present in 57% of the samples near the mid-shelf depths and decreased in samples from both shallower and deeper bathymetric classes (Table 15).

Relation to Sediments

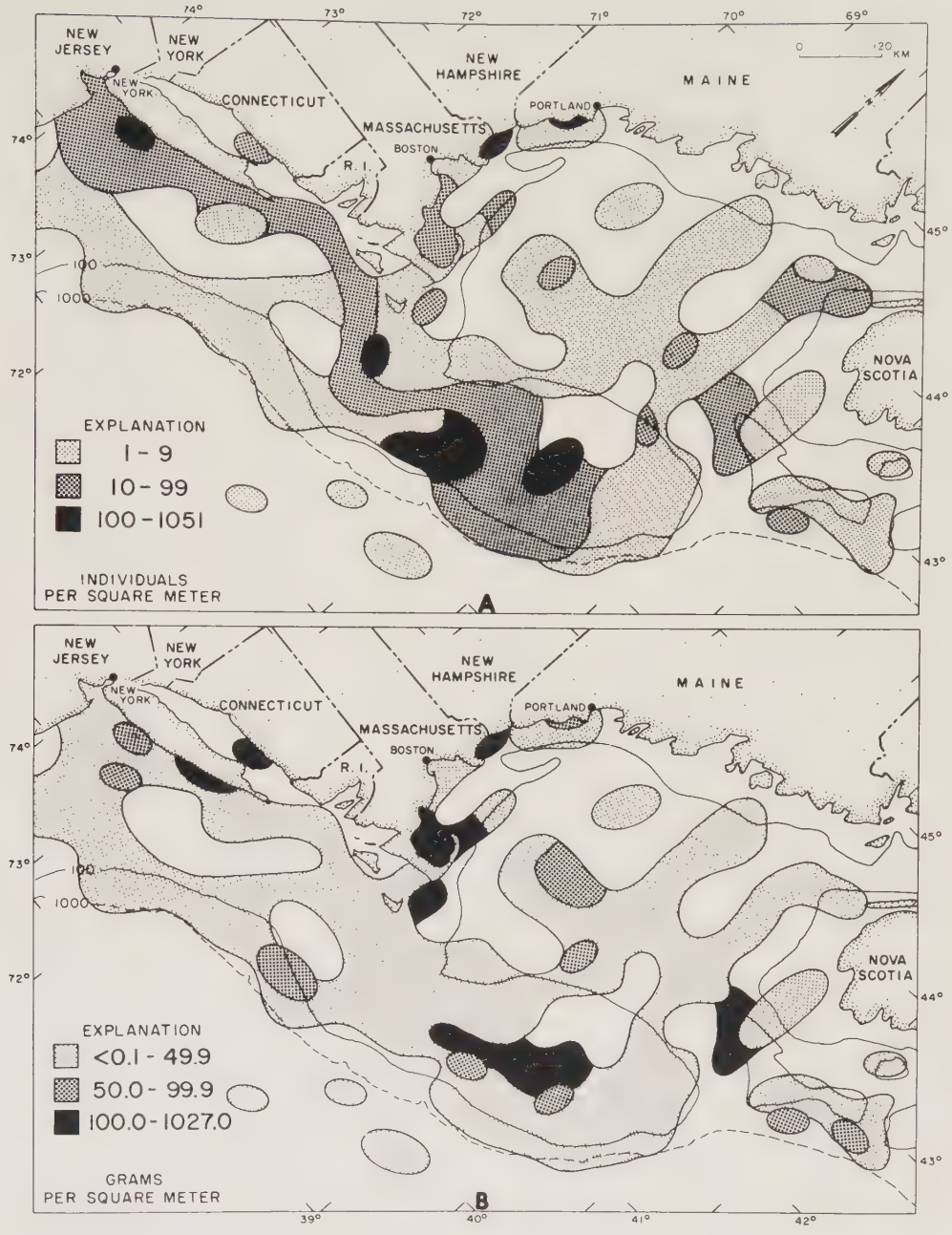
The correlation of echinoids with sand substrates was exceedingly high (Table 16; Fig. 217). Although they were present in all other types of sediments, their density averaged 67 individuals/m^2 in sand but only 3.4 or less per square meter in other sediments.

Precisely the same pattern was revealed for biomass. The average biomass in sand sediments was 81 g/m^2; in all other sediments the biomass of echinoids averaged 7.3 g or less/m^2 (Table 18; Fig. 217). The proportion of the total benthic biomass that was formed by echinoids in the sand sediments was 33%, which is an exceptionally large contribution for one taxon (Table 19).

The occurrence of echinoids in the samples was moderate to low in all sediment types (Table 20). As expected, it was highest (47%) in sand substrates. Somewhat unexpectedly, the incidence rate was lowest (8%) in sand-silt sediments and relatively high (32%) in till.

Relation to Water Temperature

Echinoids were most abundant in terms of both density and biomass in areas where the annual range in bottom water temperature was moderate, 12° to 15.9°C.



ECHINOIDEA

Figure 214

Geographic distribution of Echinoidea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

Echinoid density averaged 93 individuals/m^2 at mid-range (Table 21; Fig. 218). From this peak the average density diminished to 1.4/m^2, where the temperature range was less than 4°C, and to about 15/m^2 where the temperature change was 20°C or more.

The biomass of urchins was distributed in essentially the same manner as their numerical density among the various temperature range groupings, with one exception (Table 23; Fig. 218). Large biomass (148 g/m^2) occurred in the mid-range; moderate biomass (about 14 to 38 g/m^2) in intermediate ranges; and small biomass (6 g/m^2) in the stable areas. The one exception was a relatively large biomass (135 g/m^2) in the broadest (20°–23.9°C) temperature range class.

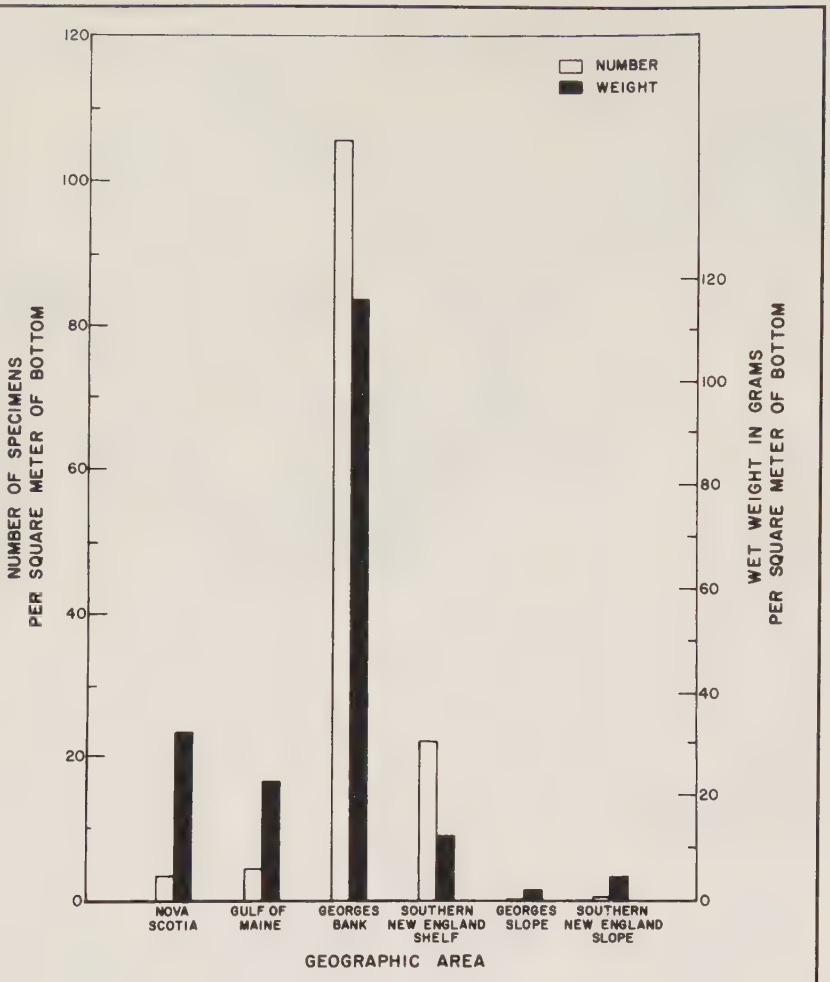


Figure 215
Density and biomass of Echinoidea in each of the six geographic areas.

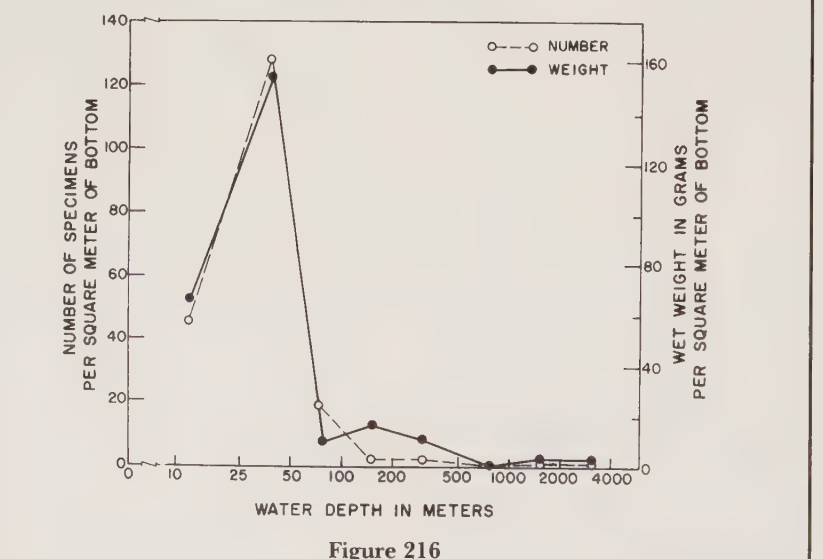


Figure 216
Density and biomass of Echinoidea in relation to water depth.

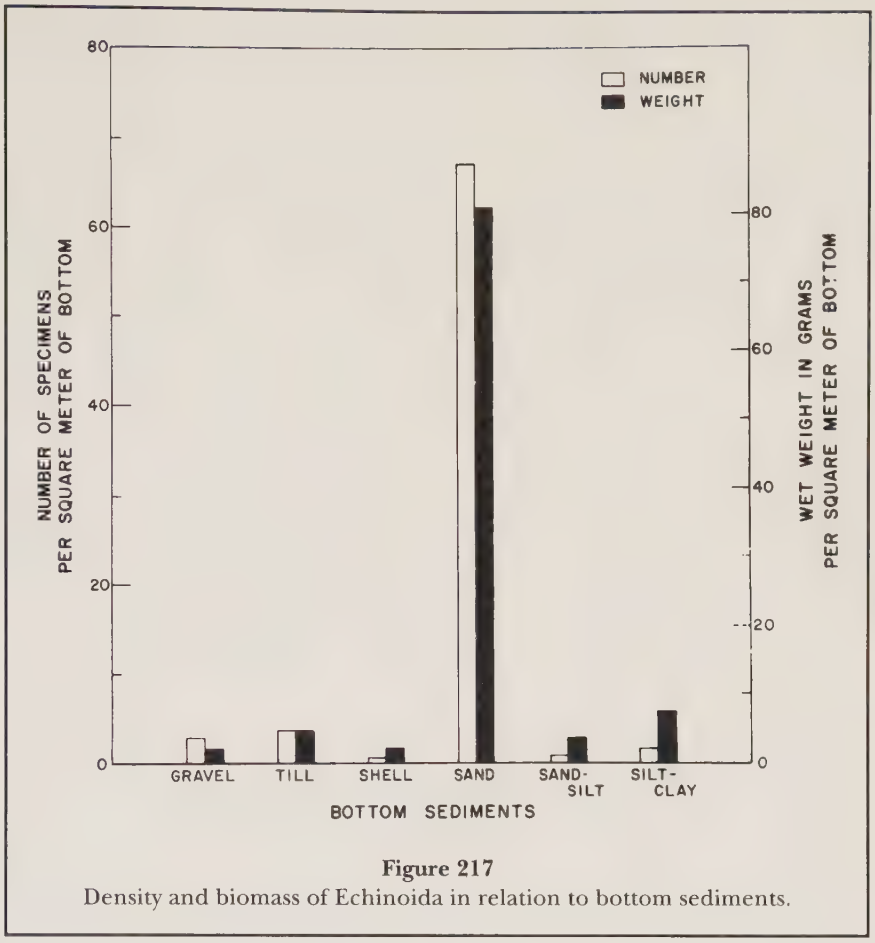


Figure 217
Density and biomass of Echinoida in relation to bottom sediments.

The proportion of the number of individuals in the total macrobenthos made up by urchins was low to moderate (0.3–5%, Table 22), but in terms of biomass they contributed extraordinarily large amounts (8–47%, Table 24) of the total.

Echinoids were present in 14 to 44% of the samples in the various temperature range classes. Frequency of occurrence, as for density and biomass, was highest in the mid-range classes and decreased in both the broader and narrower range classes (Table 25).

Relation to Sediment Organic Carbon

Echinoids showed a marked preference for low levels of sediment organic carbon and were entirely absent where levels of 2% or more prevailed. Their density was highest, but only at moderate levels (24 individuals/m^2), in the lowest carbon content class (0.01–0.49%) and fell off drastically where organic carbon was absent (2.6/m^2), as well as in the classes between 0.50 and 1.99% where density ranged from only 0.6 to 1/m^2 (Table 26; Fig. 219).

Biomass was similarly distributed among the carbon content classes. The lowest content class contained nearly 28 g/m^2 and biomass values fell off markedly in adjacent classes (Table 28; Fig. 219).

Frequency of occurrence of echinoids in the samples was generally low, ranging between 6 and 34%, and paralleled the trend exhibited by density and biomass measures (Table 30).

Ophiuroidea—Ophiuroids formed a moderately small but significant component of the New England benthos. On the average they made up about 3% of the number of animals and 2% of the biomass in the total macrobenthos.

Two orders of ophiuroids (Euryalae—basketstars, and Ophiurae—brittlestars) inhabit the study area. The basketstars have a limited distribution within the region and are relatively rare. Brittlestars, however, are widely distributed and form the bulk of all ophiuroids in our collections. They have the greatest diversity of species of all echinoderm groups; more than a score of species have been identified within the region.

The size of brittlestars in our samples ranged from large specimens of *Ophiomusium,* with disc diameters of

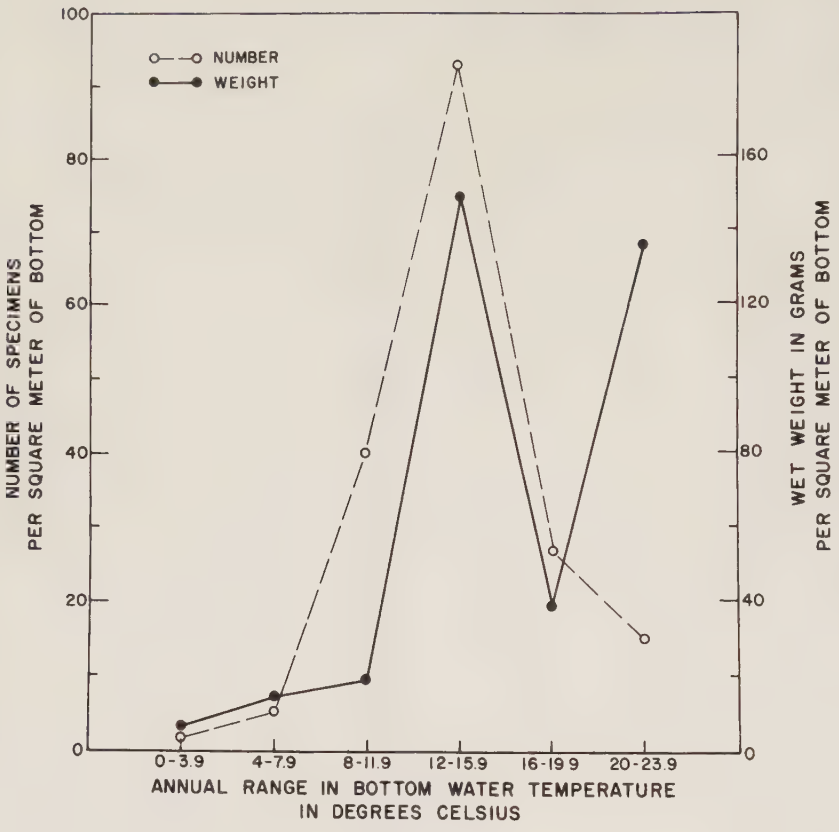


Figure 218
Density and biomass of Echinoidea in relation to the annual range of bottom water temperature.

about 25 mm and arm lengths over 12 cm, to small specimens of *Amphipholis* and *Ophiura,* with disc diameters of less than 2 mm and arms 10 mm long.

The coloration exhibited by ophiuroids in our samples was varied. Some genera, such as *Ophiura* and *Ophiomusium,* were uniformly whitish or light gray. Others were more colorful because of their mottled patterns of contrasting hues, including dark red, pink, brown, and orange. Among the more brightly colored genera were *Ophiopholis, Amphiura,* and *Ophioscolex.*

Ophiuroids obtain their food by a variety of different feeding methods; feeding types represented in our samples were carnivores, detritus feeders, filter feeders, and omnivores. A large share of the New England species generally combines the ingestion of bottom material with selective carnivorous feeding. The diet thereby consists of detritus, diatoms, and other small-size foods, as well as polychaete worms, crustaceans, bivalve mollusks, and other similar types of organisms. Brittlestars, in turn, are preyed upon by other echinoderms, but most significantly by demersal fishes.

Ophiuroidea occurred in 487 samples (45% of the total). Their density averaged 44.2/m^2 and their biomass averaged 3.26 g/m^2 (Table 5).

Geographic Distribution

Brittlestars occurred over approximately three-fourths of the study area (Fig. 220). Their average density over most of their range was between 1 and 49 individuals/m^2. High densities (100 to 680/m^2) were widespread along the outer continental shelf south of Nantucket Shoals. Brittlestars were absent from large portions of central Georges Bank, Nantucket Shoals, and much of the New York and New Jersey region.

Biomass distribution of ophiuroids tended to parallel their density distribution. Moderate (1–10 g/m^2) and large (10–80 g/m^2) biomasses were widespread off Southern New England on the outer continental shelf, and in the eastern Gulf of Maine.

The average density of ophiuroids was moderate to moderately high in all six standard geographic areas (Table 6; Fig. 221). Highest average density (94/m^2)

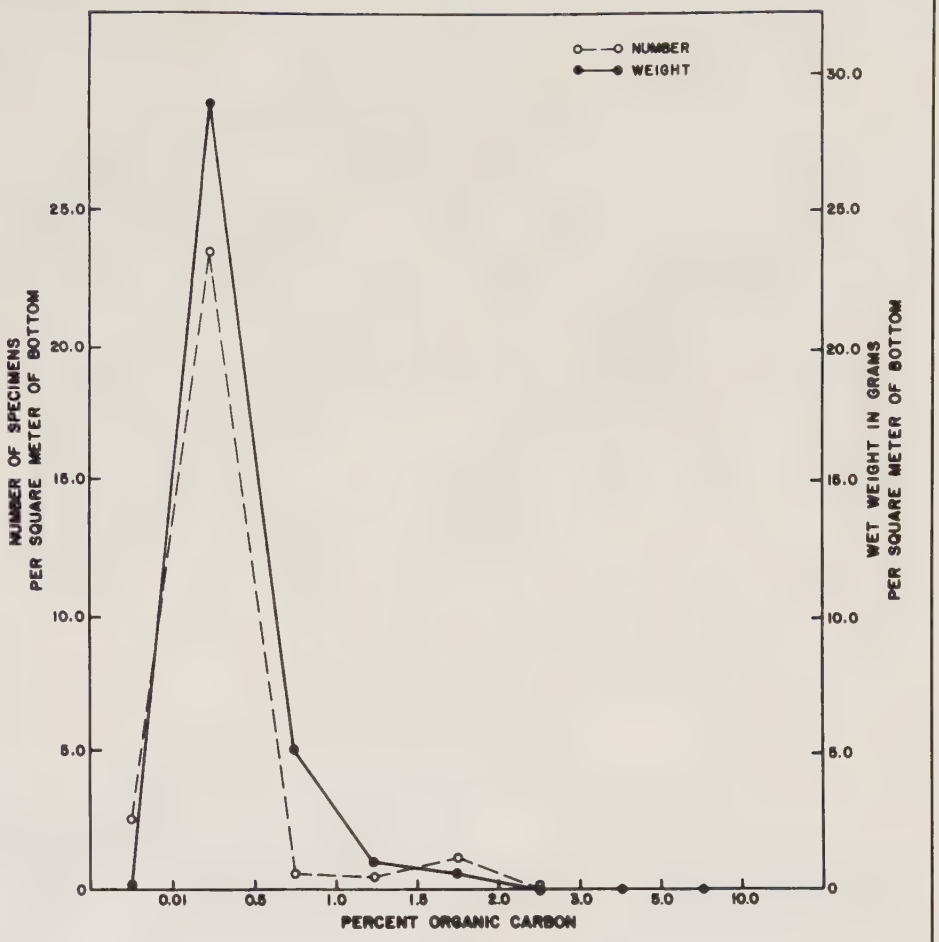


Figure 219
Density and biomass of Echinoidea in relation to sediment organic carbon.

occurred on the Southern New England Shelf, and a moderately high density (30/m^2) occurred in the Gulf of Maine. In the four remaining areas the density was moderate (14 to 17 individuals/m^2) and about equal.

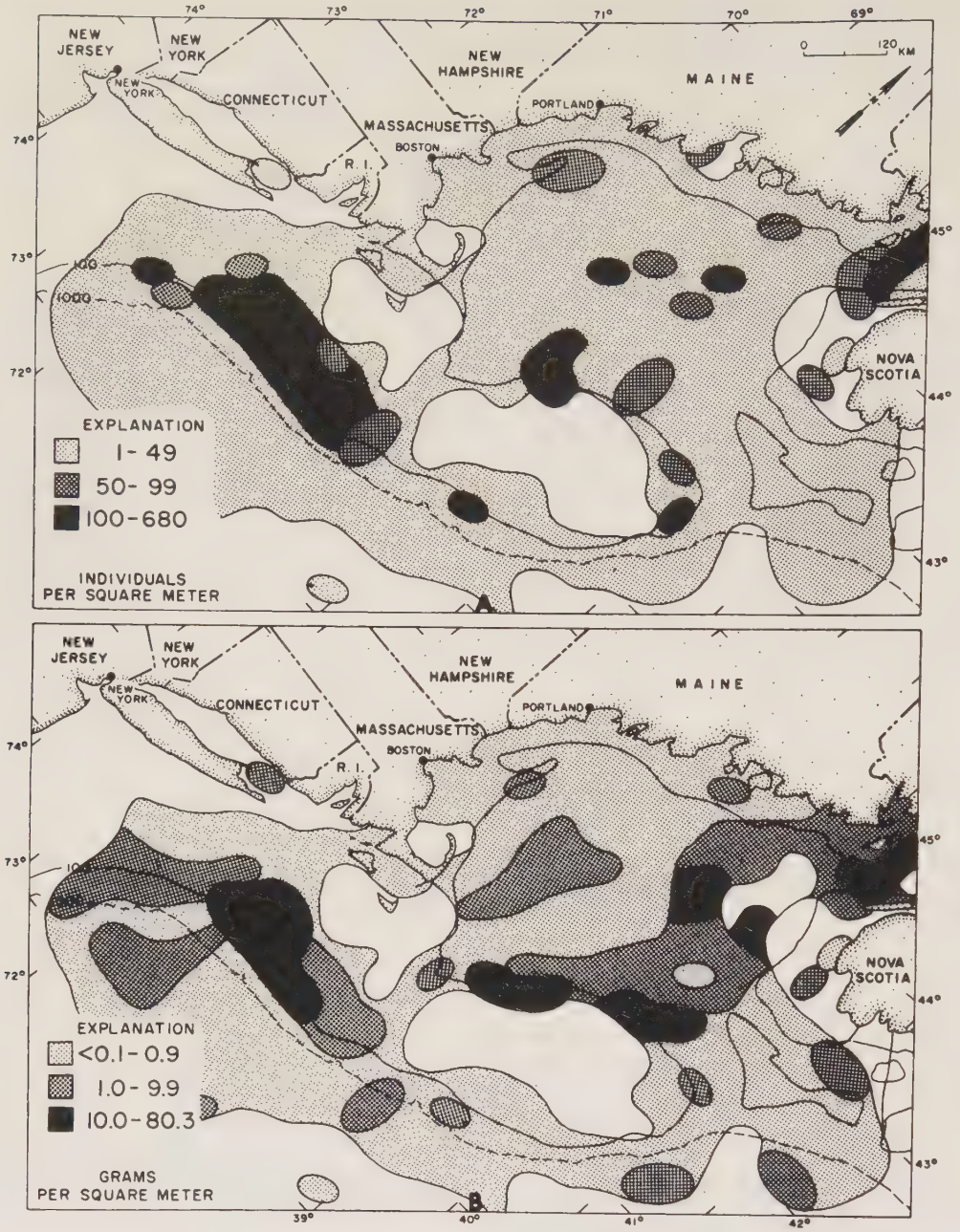
The biomass of ophiuroids, also, was relatively uniform from one area to another; total range was 0.8 to 5.4 g/m^2 (Table 8; Fig. 221). Relatively large biomasses (3.3 and 5.4 g/m^2) were encountered on the Southern New England Shelf and in the Gulf of Maine. Smallest (0.8 g/m^2) biomass was on Georges Slope. Although the average ophiuroid biomass on the Southern New England Slope was 2.6 g/m^2, an intermediate quantity, the proportion of the total fauna it made up was 13.5%, a much higher proportion than that for any other area (Table 9).

Frequency of occurrence of these organisms was moderately low (22 to 35%) in the samples from Georges Bank and, surprisingly, on the Southern New England Shelf. Ophiuroids were present in 55 to 64% of samples from all other areas (Table 10).

Bathymetric Distribution

Ophiuroids were taken at depths ranging from 13 to 3,820 m. Their density distribution revealed a pronounced zone of high abundance (35 to 87 individuals/m^2) at depths between 50 and 500 m (Fig. 222). Lower densities (0.8 to 6.2/m^2) prevailed in both deeper and shallower water. The lowest density occurred in the shallowest depth zone, 0 to 24 m.

The biomass of ophiuroids was more uniform among the various depth classes than was density; however, the same general trend was clearly evident (Table 13; Fig. 222). Biomass was relatively large (2.5 to 7.5 g/m^2) at depths between 50 and 500 m, and smaller in both deeper and shallower water.



OPHIUROIDEA

Figure 220

Geographic distribution of Ophiuroidea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

Occurrence of ophiuroids was low (9 to 10%) in samples from the inner continental shelf, at depths less than 50 m (Table 15). At depths of 50 to 500 m, where ophiuroids were most abundant, their occurrence in the samples was substantially higher, 40 to 72%. In water deeper than 500 m, ophiuroids were present in a slightly higher proportion of samples (44 to 76%). This indicates that these organisms were more uniformly distributed at a lower density in deepwater regions than they were in shallow water.

Relation to Sediments

Ophiuroids were rather plentiful in all types of bottom sediments, but trends in density and biomass in the

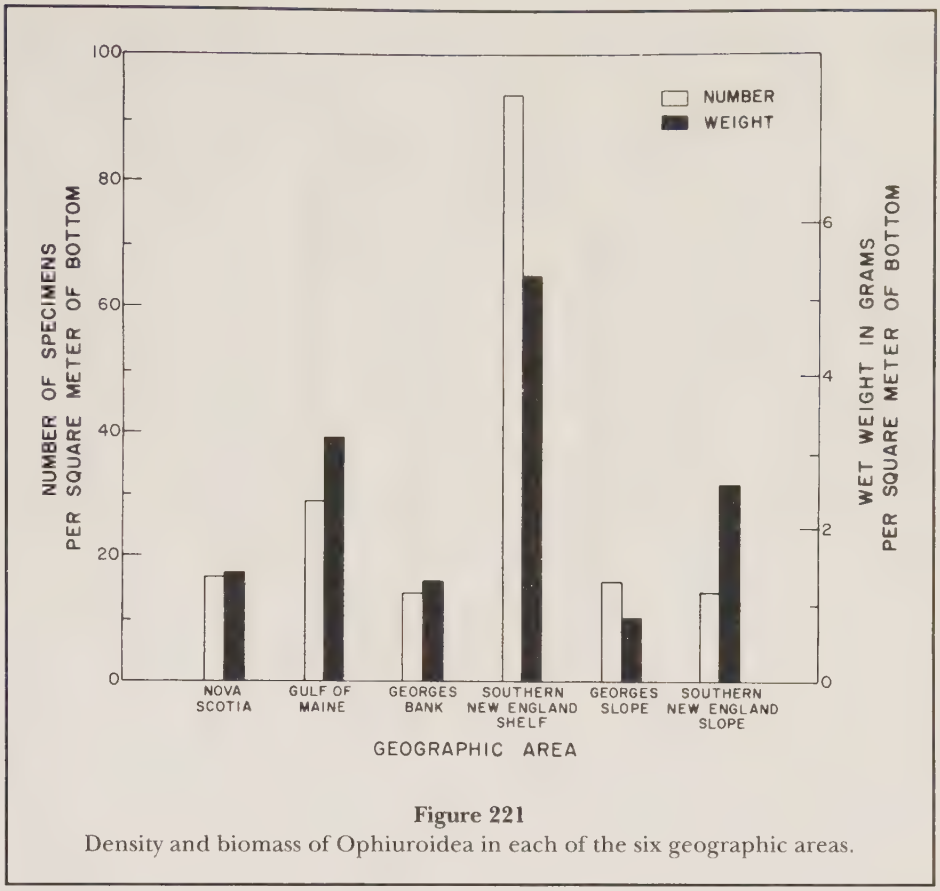


Figure 221
Density and biomass of Ophiuroidea in each of the six geographic areas.

different types were evident. Densities were low (16 to 26 individuals/m^2) in gravel, sand, and shell; intermediate (38 and 58/m^2) in till and silt-clay; and high (94/m^2) in sand-silt (Table 16; Fig. 223).

The trend of biomass in relation to sediment type was nearly the same as that revealed by density. Small biomasses of ophiuroids occurred in gravel, sand, and shell; intermediate quantities were found in silt-clay; and largest biomasses (5.3 and 5.8 g/m^2) occurred in till and sand-silt (Table 18; Fig. 223).

Occurrence of ophiuroids in the samples revealed a pattern similar to those of both density and biomass. They were present in a relatively small proportion (29–40%) of the samples from gravel, shell, and sand, and they were present in a substantially larger share (62–68%) of the samples in till, sand-silt, and silt-clay (Table 20).

Relation to Water Temperature

Ophiuroid density, biomass, and frequency of occurrence all conformed generally to the same trend of high abundance where the temperature range was less than 16°C, and low abundance

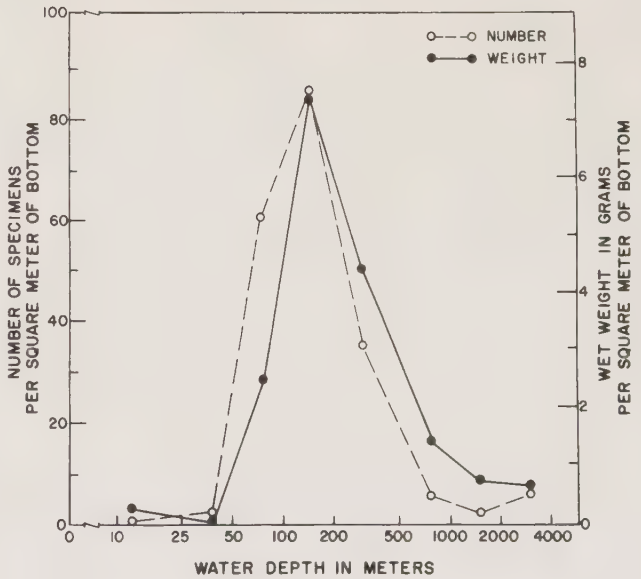


Figure 222
Density and biomass of Ophiuroidea in relation to water depth.

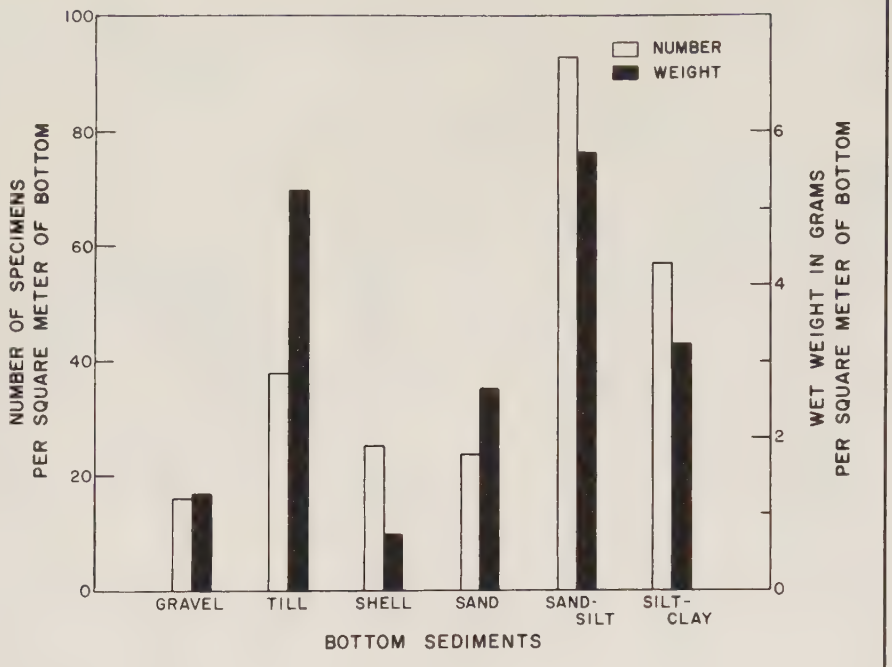


Figure 223
Density and biomass of Ophiuroidea in relation to bottom sediments.

where the range was greater than 16°C. Average density of ophiuroids increased from 25 to 74 individuals/m^2 as the range in temperature increased from less than 4°C to 12°–15.9°C, then dropped precipitously to less than 3/m^2 in the two broadest temperature range classes (Table 21; Fig. 224).

Biomass values were an order of magnitude lower than those of numerical density, but they revealed a general decline associated with an increased range in temperature (Table 23; Fig. 224). Where the temperature range was less than 12°C, the average biomass was about 3 to 6 g/m^2. Where the temperature range was greater than 16°C, the biomass averaged about 0.5 g or less/m^2.

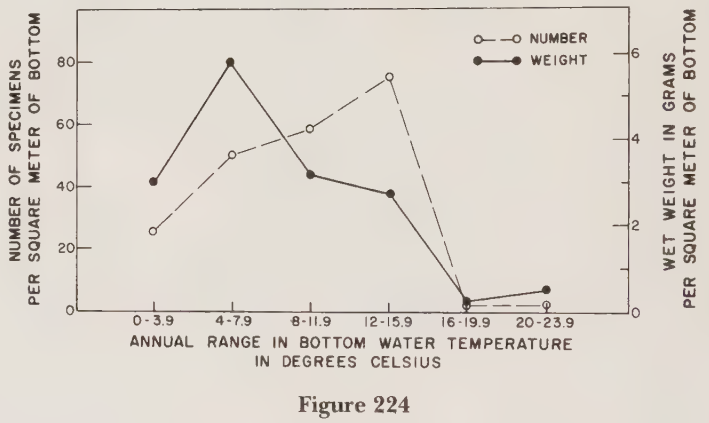


Figure 224
Density and biomass of Ophiuroidea in relation to the annual range of bottom water temperature.

Frequency of occurrence diminished rather consistently with increased range in water temperature (Table 25). Ophiuroids occurred in 64% of the samples in areas where the temperature range was less than 4°C and declined steadily to 11% in areas where the range in temperature was 20°C or more.

Relation to Sediment Organic Carbon

Ophiuroids were numerically most abundant (72 to 81 individuals/m^2) where the organic carbon content was between 0.50 and 1.49% (Table 26; Fig. 225). Average density declined in both lesser and greater amounts of organic content, with the lowest density (5/m^2) occurring in the highest content class they occupied (2.00–2.99%).

Biomass showed a similar trend but at considerably lowered magnitude (Table 28; Fig. 225). Biomass was from 5 to 6 g/m^2 in areas of organic carbon content between 0.5 and 1.49% and fell off sharply to consider-

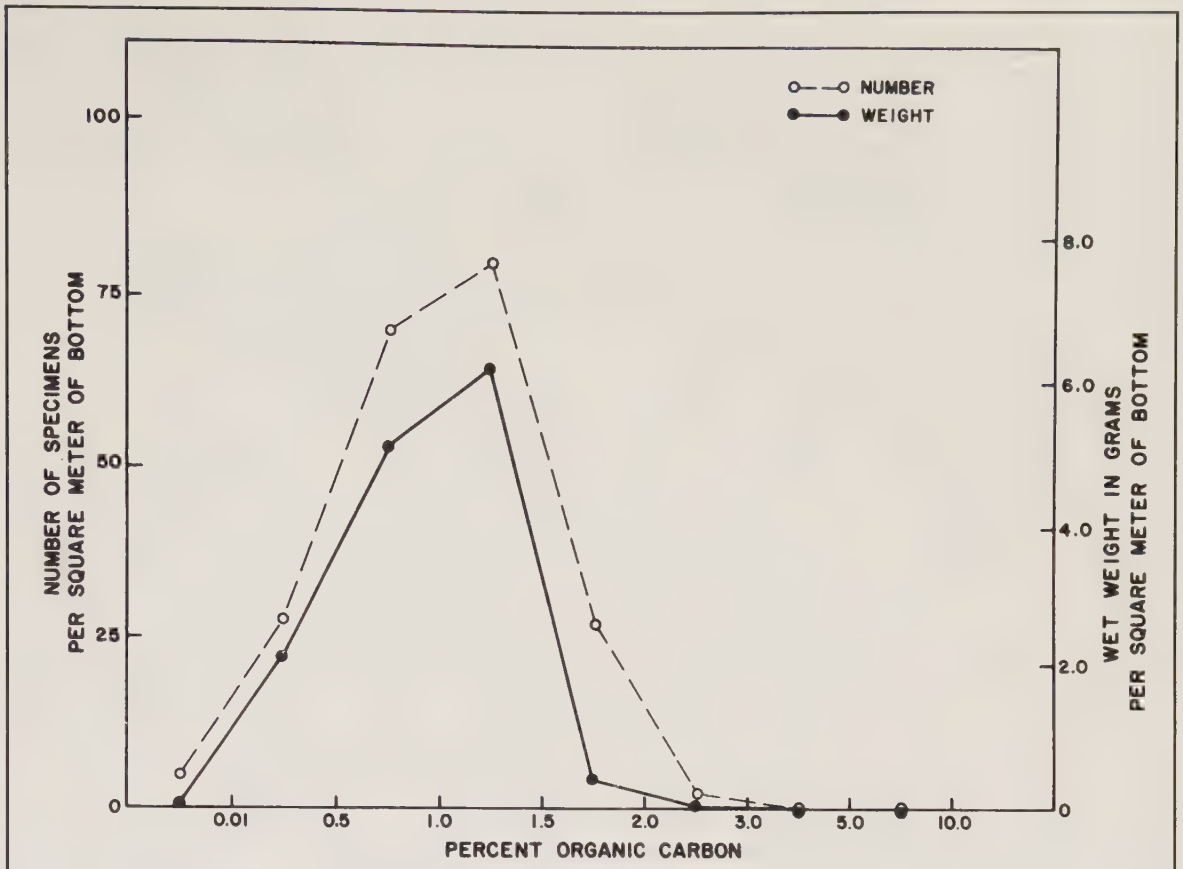


Figure 225
Density and biomass of Ophiuroidea in relation to sediment organic carbon.

ably lower levels (0.1–2 g/m^2) in classes on either side of these.

Occurrence of ophiuroids in the samples was moderate to moderately high (66–70%) in the two mid-range content classes and in the absence of measurable carbon, and moderately low (23 to 47%) in the other content classes they occupied (Table 30).

Asteroidea—Starfishes constituted a moderately small portion of the New England benthos. Their contribution to the total number of specimens was only 0.1%, but they provided 1.2% of the total biomass (Table 3).

Representatives of three orders of the Asteroidea were present in our samples: Phanerozonia, Spinulosa, and Forcipulata. All three orders contained species that were common in the samples.

Starfishes exhibited considerable variation in color, both inter- and intraspecifically. The most brightly colored species encountered was *Porania insignis*, which commonly was a deep, rich claret color with patches of whitish and yellowish papillae. Other specimens of the same species and other species within the same genus were much paler, even a drab brownish-gray. Other colorful genera encountered were *Hippasterias* and *Solaster*. Many of the more common genera, such as *Asterias*, *Astropecten*, and *Ctenodiscus*, were predominantly tan, brown, or olive.

Sizes ranged from juvenile specimens of various species that were 2 to 3 mm in radius to large specimens of *Asterias* and *Solaster* with radii of over 18 cm. Specimens with radii over 8 cm were uncommon.

Average weight of individual specimens was 1.4 g, which was large compared with other taxonomic groups.

The majority of starfishes in this region are carnivores, particularly the selective, predatory type of carnivore. Deposit feeding and filter feeding are adaptations of only a few species, some of which are locally abundant. Bivalve mollusks appear to be the principal food of New England starfishes, although a variety of small invertebrate species, as well as dead fish, are consumed. A few species of starfishes are serious predators of oysters, clams, mussels, and other commercially valuable mollusks.

Asteroids occurred in 144 samples (13% of the total). Their density averaged 1.5/m^2 and their biomass averaged 2.1 g/m^2 (Table 5).

Geographic Distribution

Starfishes had a moderately broad areal distribution in the study area (Fig. 226). They occurred in an especially large proportion of the samples from offshore Southern New England and the southern part of Georges Bank but were noticeably absent or sparse in the central Gulf of Maine, central Georges Bank, off New Jersey and along most of the continental rise.

Asteroid density was generally low throughout the New England region, averaging only 1 to 19/m^2. The slightly higher densities of 10 to 19/m^2 occurred only in the coastal and near-coastal zones. Biomass of starfishes was relatively high compared with their numerical abundance, and although they averaged less than 10 g/m^2 over most of their range, there was a substantial number of localities where the average biomass was between 10 and 105 g/m^2. The rather high biomass (10 to 50 g/m^2) along the outer margin of the continental shelf off Southern New England corresponds to the distribution of sand in that area (see Fig. 7).

Differences in starfish density among the six standard geographic areas was moderate—extremes of mean density were 0.2 and 2.5/m^2 (Table 6; Fig. 227). Densities of starfishes were generally higher in the continental shelf areas than they were on the continental slope. Indications of a north–south trend were revealed by a low density in the Nova Scotian shelf area, intermediate values in the Gulf of Maine and Georges Bank region, and relatively high density in Southern New England.

Biomass distribution was similar to density. There were only two geographic areas in which the biomass was unusually small (0.02 and 0.05 g/m^2), the two slope areas (Table 8; Fig. 227). Relatively high biomasses (1.0 to 4.5 g/m^2) occurred in the continental shelf areas.

Disparity in the average size of starfishes from the different areas was substantial. For example, in the Nova Scotia area the average weight of individuals specimens was 1 g, whereas in the slope areas, they averaged only 0.1 g each.

The frequency of occurrence of starfishes was low (6 to 19%) in all geographic areas (Table 10).

Bathymetric Distribution

Asteroids occurred at depths ranging from 13 to 2,329 m, and at a mean depth of 184 m. They occurred in substantially higher densities (1.8 to 2.5/m^2) at depths between 25 and 200 m than at other depths (Table 11; Fig. 228). In very shallow water (less than 25 m) and in depths beyond the continental shelf their density was 0.1 to 0.7/m^2. Densities were generally lowest in the deepest water. The maximum density of 167/m^2 was encountered at a depth of 49 m.

Starfish biomass varied considerably from one depth class to another, but the distributional pattern was similar to that described above for density (Table 13; Fig. 228). The average biomass on the continental shelf was 3 to 4 g/m^2 (except in the 25–49 m depth class where the biomass was unusually small). In depths below 200 m, the biomass averaged 0.04 g or less per square meter but was slightly higher on the lower continental slope and continental rise than on the middle and upper continental slope.

The proportions of samples in the various depth classes that contained starfishes ranged from 5 to 20% (Table 15). Their frequency of occurrence was slightly higher between 50 and 200 m than at other depths.

Relation to Bottom Sediments

Starfishes were taken in all sediment types except shell, and there were marked differences in quantity between samples from fine-texture sediments compared with those from coarse sediments (Table 16; Fig. 229). Largest quantities were from fine-grain sediments.

Average density in the coarse substrates (till and gravel) was 0.2 and 0.8/m^2, respectively. In the finer substrates (sand, sand-silt, and silt-clay) asteroids averaged 1.3 to 1.8/m^2.

Asteroid biomass was 0.5 g or less per square meter in the coarse sediments and 2.0 to 3.6 g/m^2 in the fine-grain sediments.

Starfishes occurred in a markedly higher proportion (14 to 16%) of samples from sediments composed of fine particles than of samples composed of gravel and till (8 and 9%) (Table 20).

Relation to Bottom Temperature

Asteroids were found in moderate to low amounts in all temperature range classes (Table 21; Fig. 230), but they were more abundant where the temperature range was moderate rather than extreme.

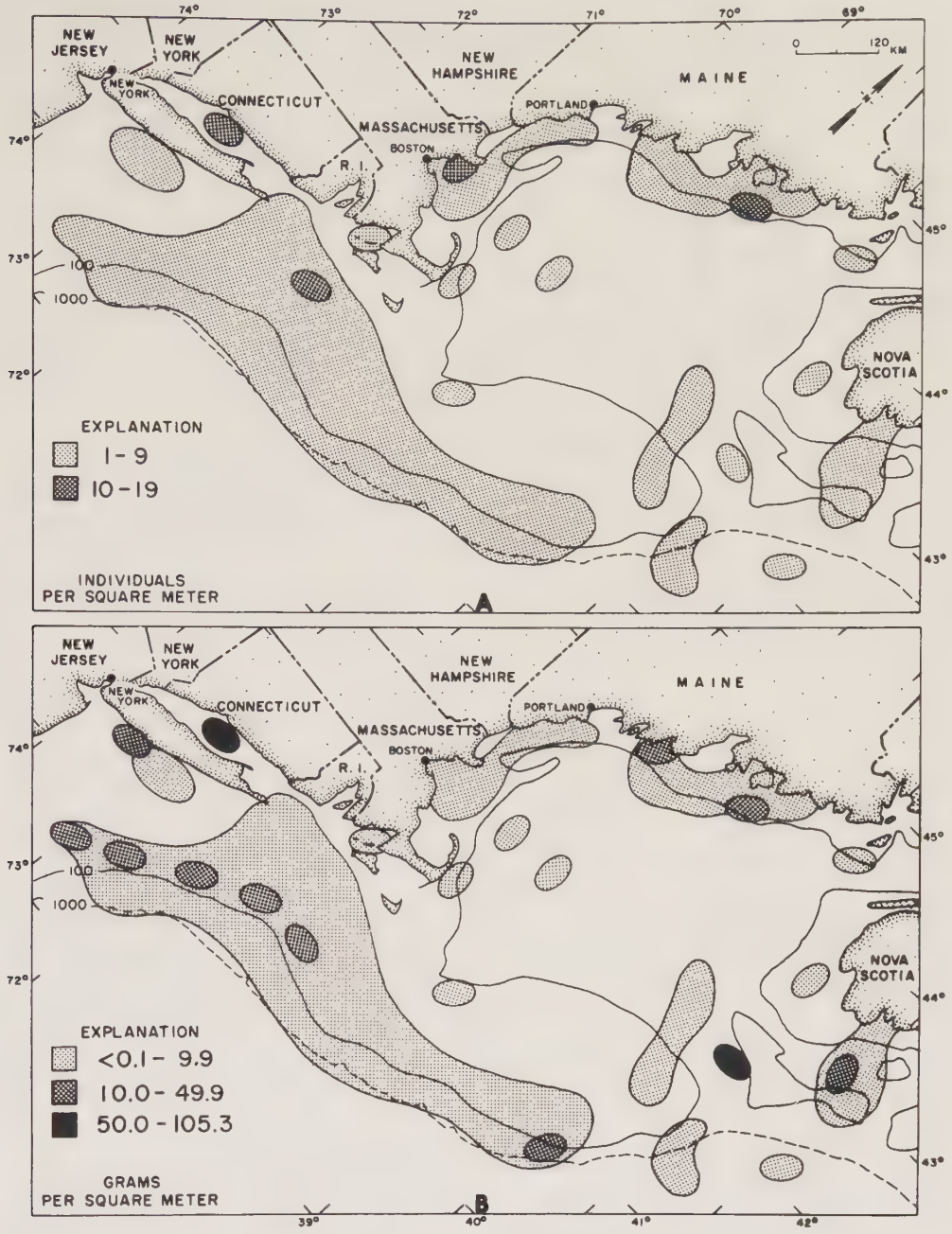
Average densities (0.4 to 0.9/m^2) of starfishes in the extreme temperature range classes (0°–3.0° and 16°–23.9°C) were considerably below those found in the mid-ranges (4°–15.9°C) where values of 1.2 to 2.7/m^2 occurred. In terms of total faunal density, asteroids provided only 0.2% or less of the total number of specimens in each of the six temperature range classes (Table 22).

The average biomass of starfishes in the intermediate temperature range classes was quite stable, varying only from 2.8 to 3.6 g/m^2; the two extreme classes, however, yielded only 0.1 to 0.5 g/m^2, respectively (Table 23; Fig. 230). Starfishes in the various temperature range classes represented from 0.1 to 4% of the total faunal biomass (Table 24).

The proportion of samples that contained asteroids was lowest (6–4%) in the two extreme temperature range classes and the highest (21%) in the 8°–11.9°C temperature range class (Table 25).

Relation to Sediment Organic Carbon

Asteroids were present in only four of the eight organic



ASTEROIDEA

Figure 226

Geographic distribution of Asteroidea: A–number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

carbon content classes. The four classes in which they occurred ranged from 0.01 to 1.99%. Average density was fairly low but relatively uniform in the three classes between 0.01 and 1.49% carbon content, ranging from 1.6 to 1.0 individuals/m^2 (Table 26; Fig. 231). The 1.50 to 1.99% class, however, contained only 0.4 individuals/m^2.

The distribution of biomass was parallel to that of density, highest (5.5 g/m^2) in the 1.00–1.49% carbon content class and dropping off significantly in higher and lower adjacent content classes where values were uniformly low, ranging from 1.03 to 1.42 g/m^2 (Table 28; Fig. 231).

Frequency of occurrence of asteroids in the samples in the organic carbon content classes ranged from 14 to

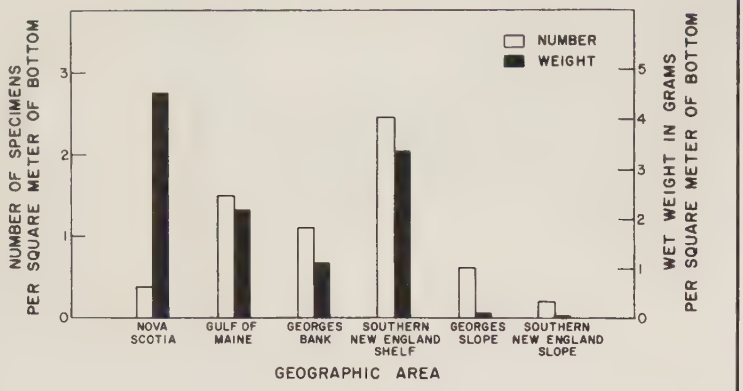


Figure 227
Density and biomass of Asteroidea in each of the six geographic areas.

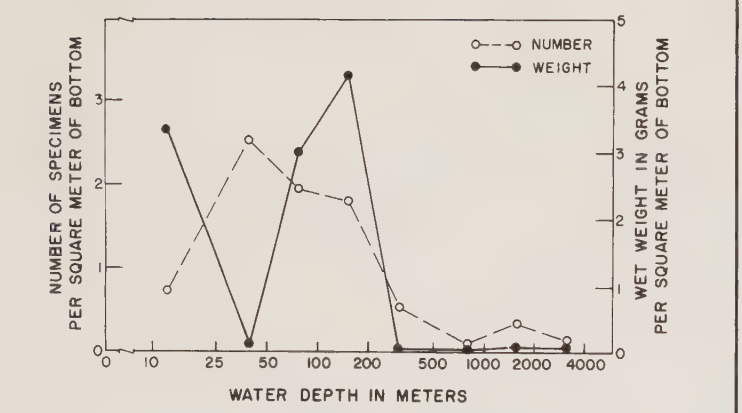

NUMBER
WEIGHT
NUMBER OF SPECIMENS PER SQUARE METER OF BOTTOM
WET WEIGHT IN GRAMS PER SQUARE METER OF BOTTOM
0 10 25 50 100 200 500 1000 2000 4000
WATER DEPTH IN METERS

Figure 228
Density and biomass of Asteroidea in relation to water depth.

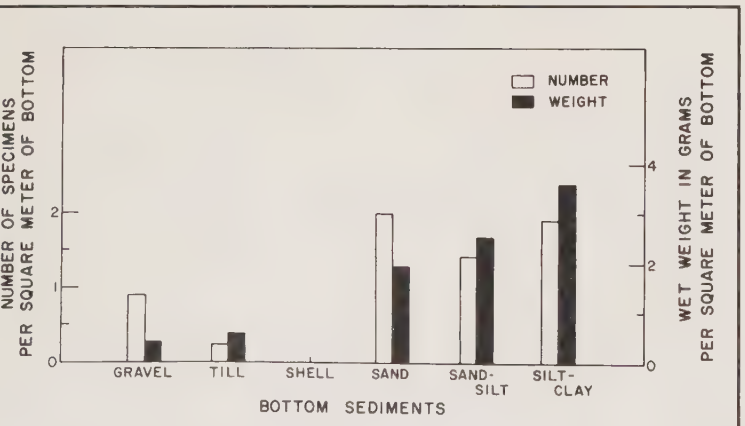


Figure 229
Density and biomass of Asteroidea in relation to bottom sediments.

17% in the three classes between 0.01 and 1.49%, and was 7% in the 1.50 to 1.99% content class (Table 30).

Hemichordata

Representatives of the phylum Hemichordata are all from one class (Enteropneusta, acorn worms) and one genus (*Balanoglossus*). A total of 101 specimens, weighing 18.7 g, were collected at 4 stations (0.4% of total); average density (0.1 individuals/m^2) and biomass (0.02 g/m^2) were very low (Table 5).

Geographic Distribution
The geographic distribution of acorn worms was restricted to the Southern New England Shelf (3 stations) and Southern New England Slope (1 station). Mean densities were 0.3 individual/m^2 or less and mean biomass 0.06 g/m^2 or less (Tables 6 and 8; Fig. 232). Frequency of occurrence of hemichordates in the samples was a very low 1% (Table 10).

Bathymetric Distribution
Acorn worms occurred in three depth range classes: 50–99 m, 100–199 m, and 500–599 m, where their mean density ranged from <0.1 to 0.5 individual/m^2 and their mean biomass was 0.01 g/m^2 in the two deepwater ranges and 0.05 g/m^2 in the mid-shelf range (Tables 11, 13; Fig. 233). Five percent of the samples in the 500–999 m depth range yielded specimens, whereas the occurrence in the other two was from <1 to 1% (Table 15). The depth range of our samples was from 79 to 567 m.

Relation to Bottom Sediments
Acorn worms were found in low abundance in sand, sand-silt, and silt-clay substrates. Mean density ranged from <0.1 to 0.2 individual/m^2 and mean biomass from <0.01 to 0.04 g/m^2 (Tables 16, 18; Fig. 234). Frequency of occurrence in the samples was <1 to only 1% (Table 20).

Relation to Bottom Temperature
Hemichordates were restricted to areas where the annual range in water temperature was less than 16°C. Mean density and biomass were very low (<0.1/m^2 and <0.01 g/m^2) in the lowest temperature range class; mean densities of 0.2/m^2 occurred in each of the two

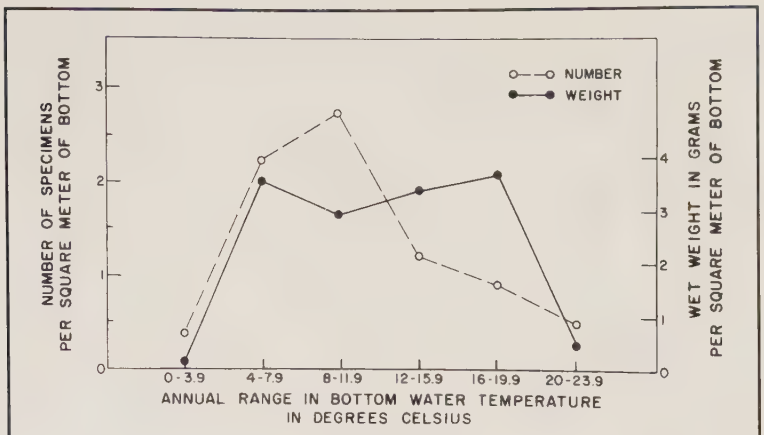


Figure 230
Density and biomass of Asteroidea in relation to the annual range of bottom water temperature.

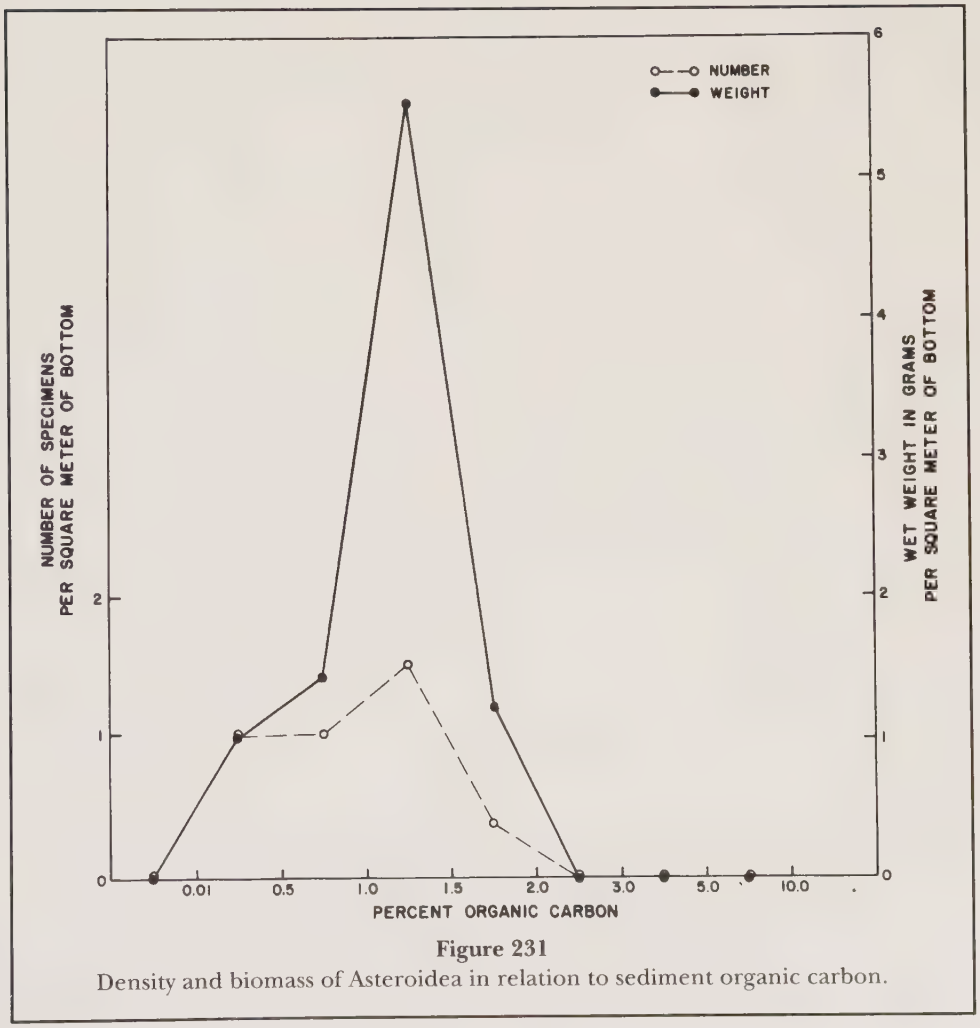


Figure 231
Density and biomass of Asteroidea in relation to sediment organic carbon.

range classes between 8 and 15.9°C. Mean biomass ranged from 0.03 to 0.04 g/m^2 (Tables 21, 22; Fig. 235). Frequency of occurrence was in the <1 to 1% range in the three range classes (Table 25).

Relation to Sediment Organic Carbon

Distribution of hemichordates was limited to the three organic carbon content classes between 0.01 and 1.49%. Mean densities were between 0.1 and 0.2 individual/m^2

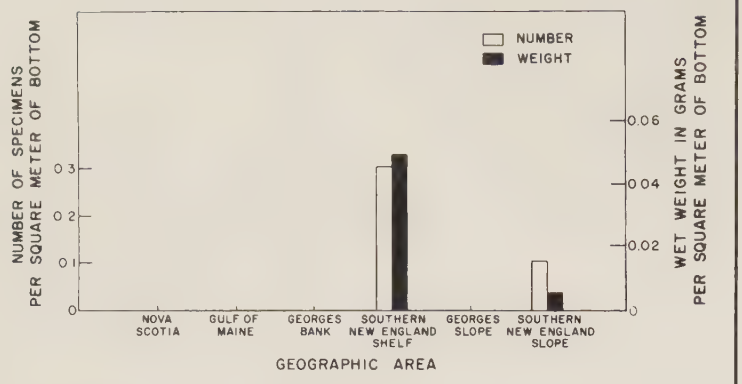


Figure 232
Density and biomass of Hemichordata in each of the six geographic areas.

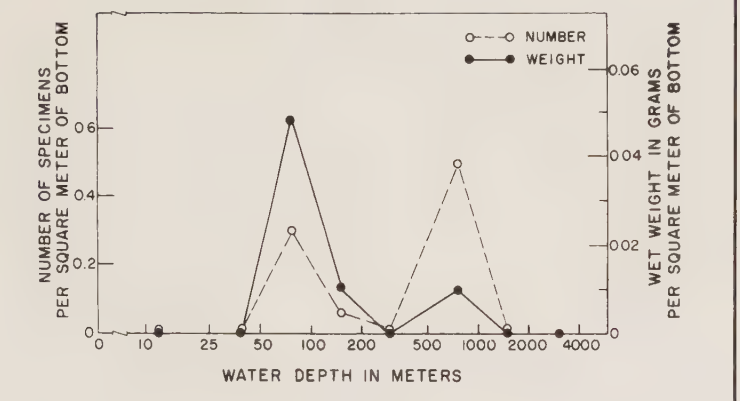


Figure 233
Density and biomass of Hemichordata in relation to water depth.

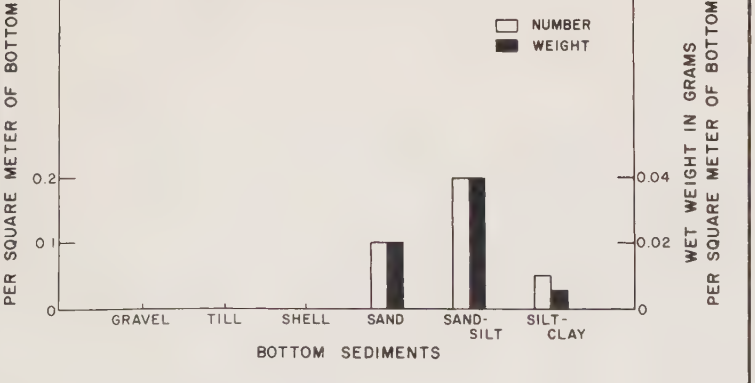


Figure 234
Density and biomass of Hemichordata in relation to bottom sediments.

and mean biomass between <0.01 and 0.03 g/m^2 (Tables 26, 28; Fig. 236). Only 1% of the samples in the three carbon content classes contained specimens of acorn worms (Table 30).

Chordata

Ascidiacea—Ascidians were moderately common in the New England benthos and constituted 1.1% of the total number of specimens and 2.2% of the total biomass (Table 3).

The size of solitary tunicates in our collections ranged from 4 mm to more than 20 cm. Although colonial forms are known to attain lengths greater than 50 cm in this region, the specimens in our samples were smaller (12 cm or less in length) than the largest solitary forms.

Interspecific variation in color of New England tunicates was rather broad, and in some groups the intraspecific variation was also considerable. The majority of species were dull olive, tan, or brown. A rather large number covered their tests with sand grains or silt that very effectively camouflaged them. A few groups contained beautifully colored species. Their coloration consisted of a blending of cream and light yellow with various shades of orange and red.

In order to control their rapid colonization on hard substrates and fouling of man-made structures, such as ship bottoms, pipes, buoys, and similar structures, the maritime industry incurs high economic costs. Ascidians occurred in 181 samples (17% of the total). Their density averaged 16.3/m^2 and their biomass averaged 4.1 g/m^2 (Table 5).

Geographic Distribution

Ascidians were distributed over large portions of the study area (Fig. 237), but their occurrence was patchy, with density changing abruptly from one locality to another. They were most common in the coastal areas and on the offshore banks and were sparse or absent from the following areas: the deeper part of the western Gulf of Maine, north-central Georges Bank, and parts of the continental shelf off Connecticut, New York, and New Jer-

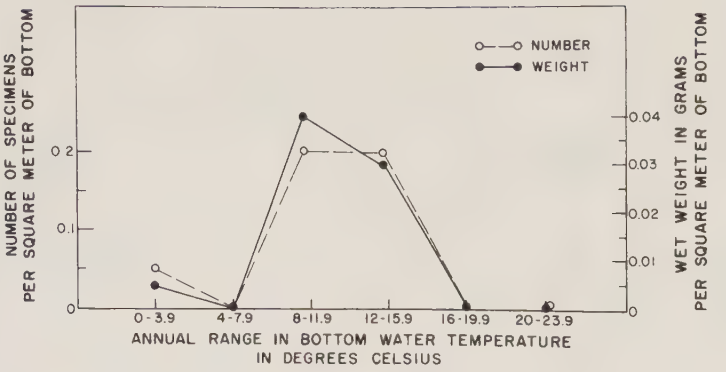


Figure 235
Density and biomass of Hemichordata in relation to the annual range of bottom water temperature.

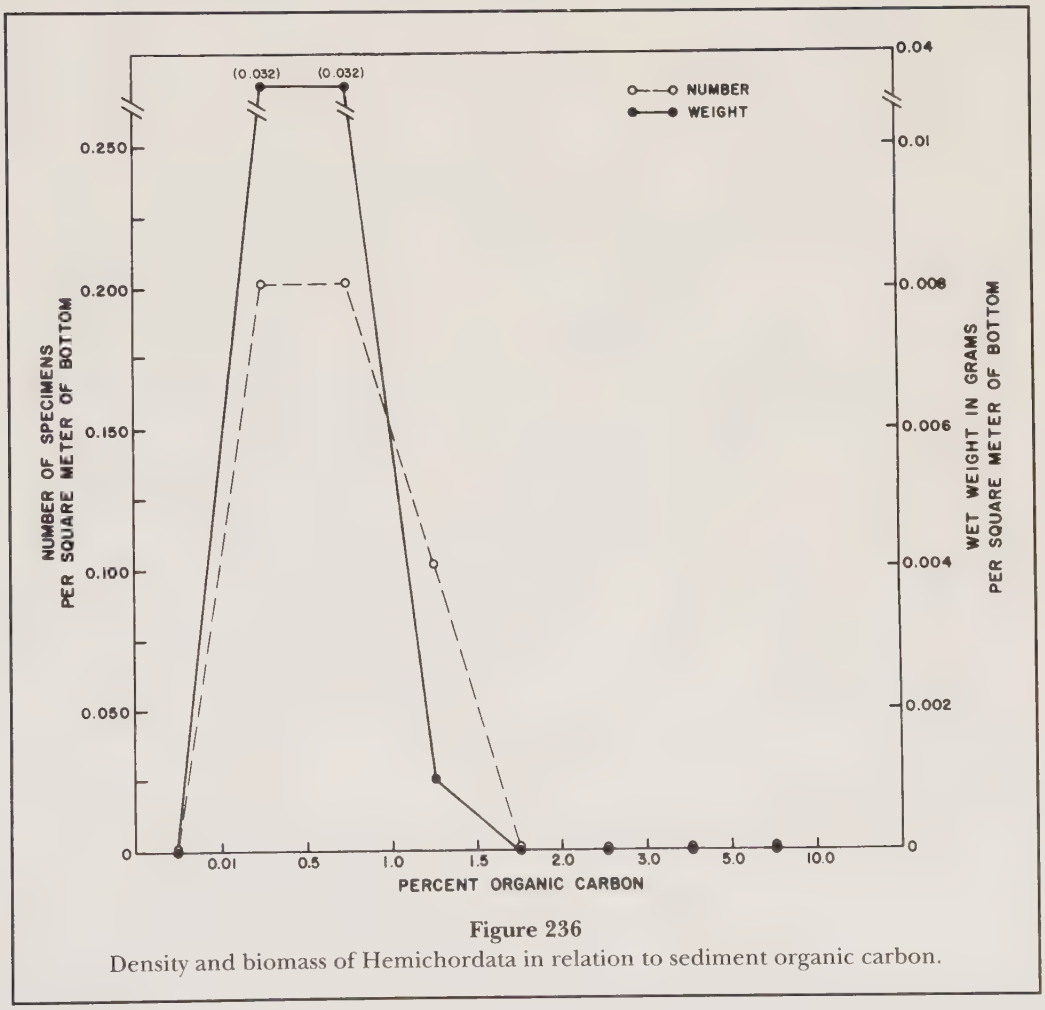
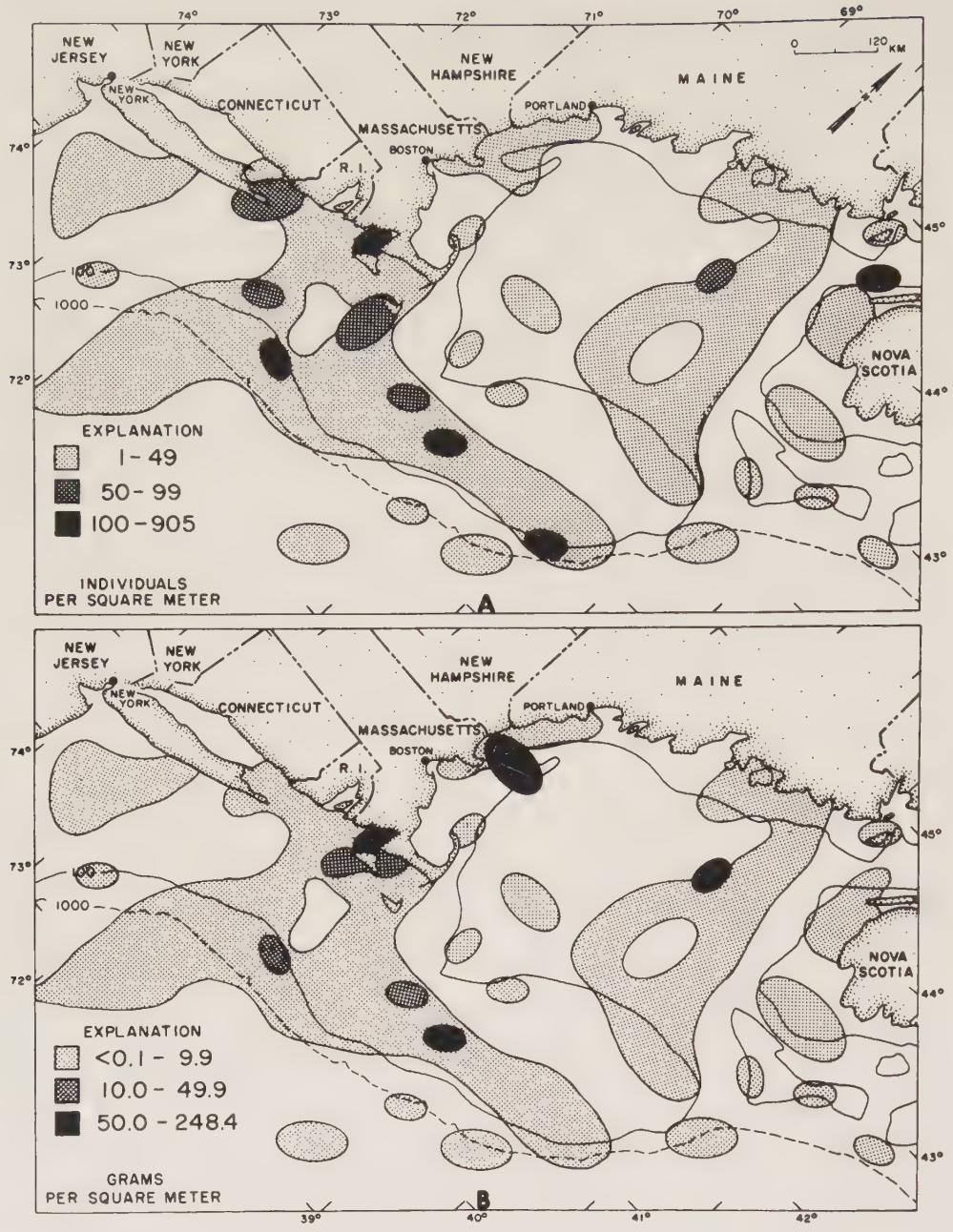


Figure 236
Density and biomass of Hemichordata in relation to sediment organic carbon.

sey. Densities throughout most of their range averaged less than 50 individuals/m^2. In a few localities, however, their density averaged between 100 and 900/m^2. Their biomass was moderate (less than 10 g/m^2) over most of their range and large quantities (50 to 288/m^2) were encountered in several different areas.

The average density of ascidians was moderately high (34 and 27 individuals/m^2) in only two of the six stan-



ASCIDIACEA

Figure 237

Geographic distribution of Ascidiacea: A—number of specimens per square meter of bottom; B—biomass in grams per square meter of bottom.

dard geographic areas, Georges Bank and the Southern New England Shelf (Table 6; Fig. 238). In these two areas the biomass also was large (5.1 and 8.4 g/m^2) (Table 8; Fig. 238). In the four other areas their average density was low (2.8 or less/m^2), and the biomass was relatively small (0.1 to 2.6 g/m^2). Biomass was especially small (0.11 and 0.17 g/m^2) in the two slope areas.

Ascidians occurred in a moderately small proportion of samples (12 to 23%) and were present in approximately the same proportion of samples from all areas (Table 10).

Bathymetric Distribution

Ascidians occurred at water depths ranging from 13 to 3,080 m, (Table 11; Fig. 239). Relatively high densities

(6 to 32 individuals/m^2) were encountered on the continental shelf; low densities (0.1 to 2.7/m^2) occurred on the continental slope and continental rise.

Biomass of ascidians, also, was larger on the continental shelf than in deep water beyond the shelf (Table 13; Fig. 239). Average biomass at water depths less than 200 m ranged between 1.0 and 8.9 g/m^2, whereas at depths greater than 200 m the biomass averaged less than 0.7 g/m^2.

Ascidians were present in the samples from nearly all depth classes at about the same low range of 5 to 24% (Table 15).

Relation to Sediments

Ascidians occurred in all six types of bottom sediments; however, their density and biomass varied substantially from one type to another (Table 16; Fig. 240). Densities were relatively high (29 and 22/m^2) on gravel and sand bottoms, and intermediate (11/m^2) in sand-silt. Densities were low (5.1 or less/m^2) in till, shell, and silt-clay.

Biomass of ascidians followed the same trend as density, but the differences were less pronounced (Table 18; Fig. 240). Average biomass was largest (9.7 to 4.4 g/m^2) on gravel and sand, intermediate in sand-silt, and small (<2 g/m^2) in the remaining sediment types.

Frequency of occurrence in the samples was moderately low (11 to 32%) in all types of bottom sediments (Table 20). In the majority of sediment categories, the small differences in occurrence rate are correlated directly with ascidian density and biomass. Shell and till values, which are based on a small number of samples, are incongruous.

Relation to Water Temperature

Although the trends of ascidian density and biomass relative to the annual range in bottom water temperature were not consistent, generally the quantities were larger where the temperature range was moderate, and smaller at both temperature extremes (Tables 21, 23; Fig. 241). In areas where the temperature range was moderate, from 8° to 19.9°C, the average density of ascidians ranged from 6 to 59/m^2 and the biomass ranged from 7 to 14 g/m^2. Where water temperature ranges were extreme, less than 8°C and more than 20°C, the average density was low (2–4/m^2) and the biomass was small (0.5–4.1 g/m^2). Two temperature range classes (8°–11.9°C and 16°–19.9°C) contained significantly greater quantities than did the other classes.

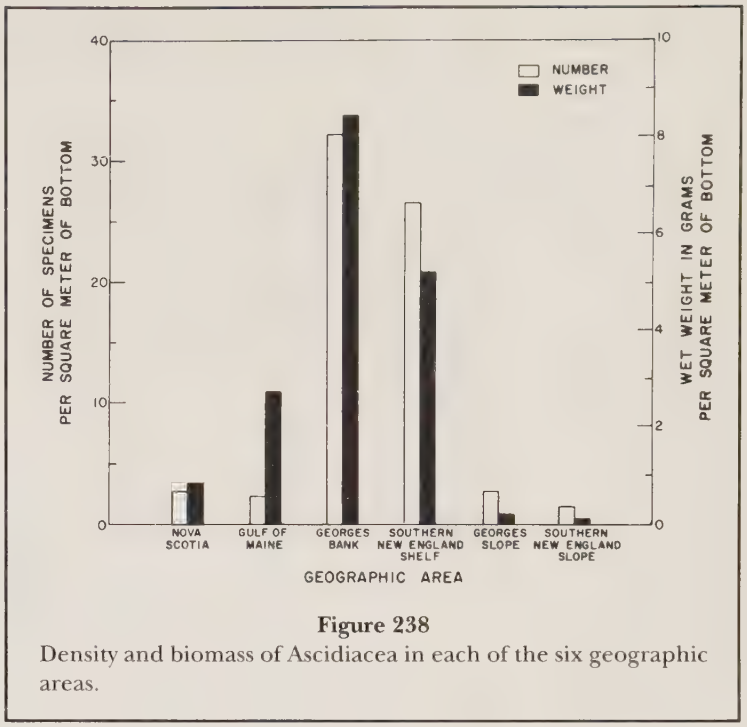


Figure 238

Density and biomass of Ascidiacea in each of the six geographic areas.

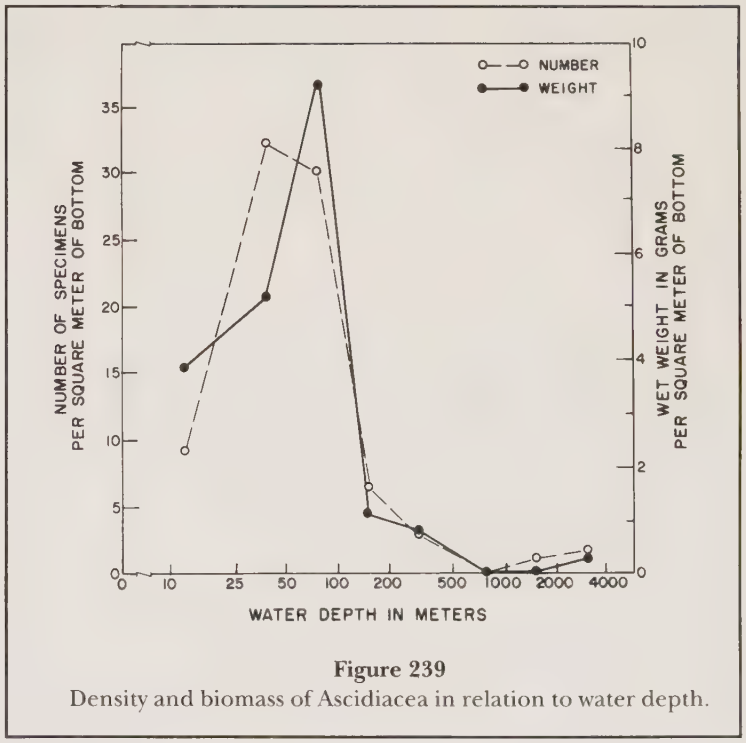


Figure 239

Density and biomass of Ascidiacea in relation to water depth.

Frequency of occurrence of ascidians was moderately low in all temperature range classes. Their occurrence rate, however, was somewhat high (17 to 24%) where the temperature range was moderate, and lower (11 to 12%) where the temperature range was very small and very large (Table 25).

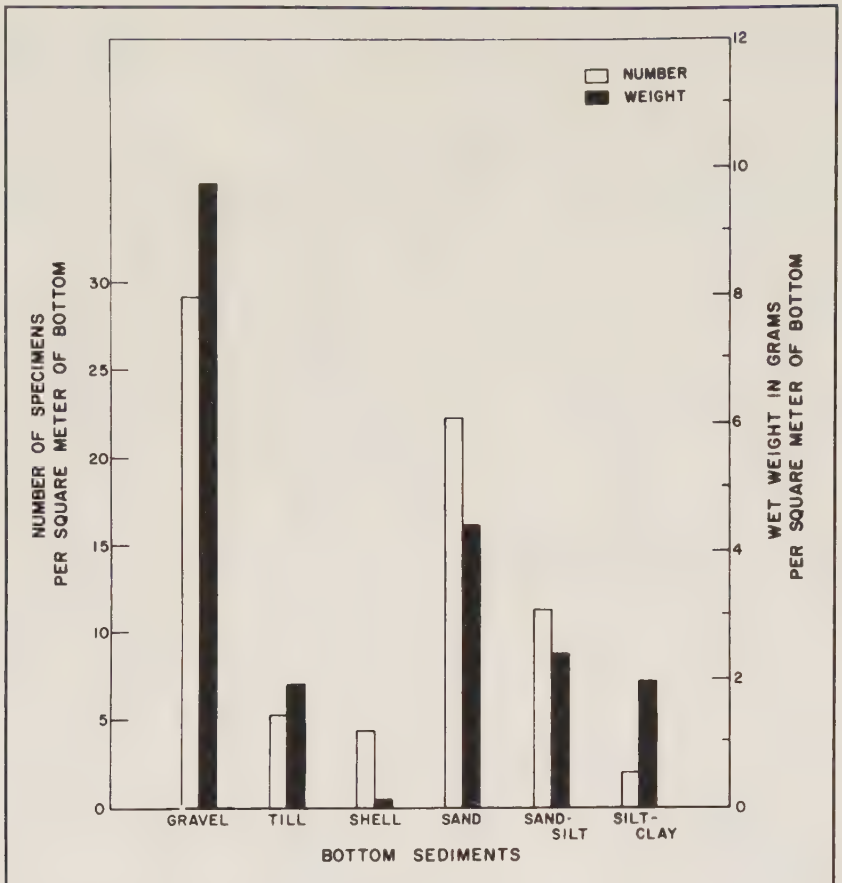


Figure 240
Density and biomass of Ascidiacea in relation to bottom sediments.

Relation to Sediment Organic Carbon

A general trend of diminishing density and biomass with increasing sediment organic carbon content was exhibited by New England region ascidians (Tables 26, 28; Fig. 242), and they were restricted to the low to mid-range carbon content classes between 0.01 and 2.99%. Mean density ranged from 21 to 4.4 individuals/m^2, and mean biomass from 4.4 to 0.2 g/m^2.

Frequency of occurrence in samples was low and paralleled the trend of density and biomass, ranging from 23% to 8% as carbon content increased (Table 30).

Dominant Components of the Macrobenthos

This section identifies and defines the dominant faunal constituents of the New England region macrobenthos and their relationship to each of the abiotic parameters considered in the treatment of each taxonomic group in the preceding sections. "Dominance," as used in this report, refers to the taxonomic group that mathematically contributed the highest number of individuals or greatest total accumulated wet weight. Results are expressed in both measures of abundance because of the marked differences that existed between them.

In spite of individual disparity in rank order within each measure of abundance, members of four taxonomic groups, collectively, made up the bulk of the macrobenthic invertebrate fauna of the New England region. The four major taxonomic components are 1) Annelida; 2) Mollusca, comprising Bivalvia, the chief component, as well as Gastropoda, Scaphopoda, Polyplacophora, and Cephalopoda; 3) Crustacea, with Amphipoda the chief component of this group, followed by Cumacea, Isopoda, Decapoda, Cirripedia, Mysidacea, Tanaidacea, Ostracoda, and Copepoda in progressively smaller proportions; and 4) Echinodermata composed of Ophiuroidea, Echinoidea, Holothuroidea, Asteroidea, and Crinoidea in diminishing proportions. Table 3 lists the contributions of each of the above taxa to the total density and biomass of the New England macrobenthic fauna.

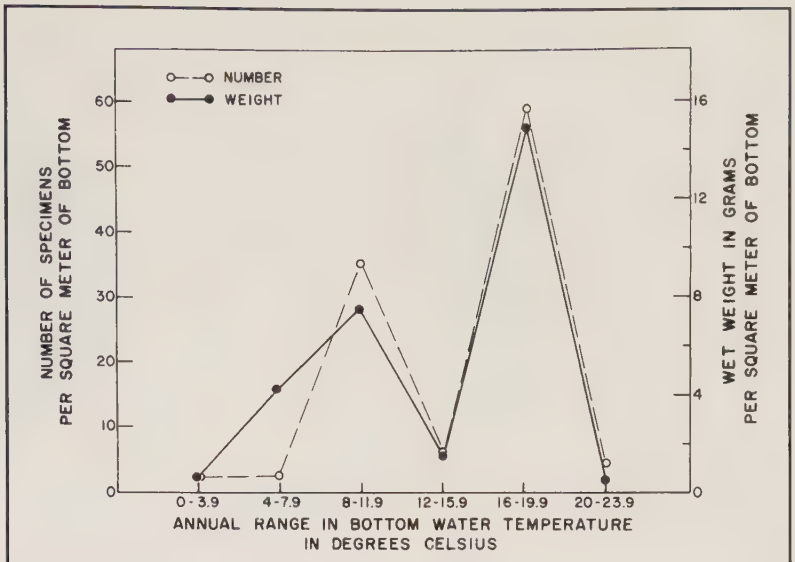


Figure 241
Density and biomass of Ascidiacea in relation to the annual range of bottom water temperature.

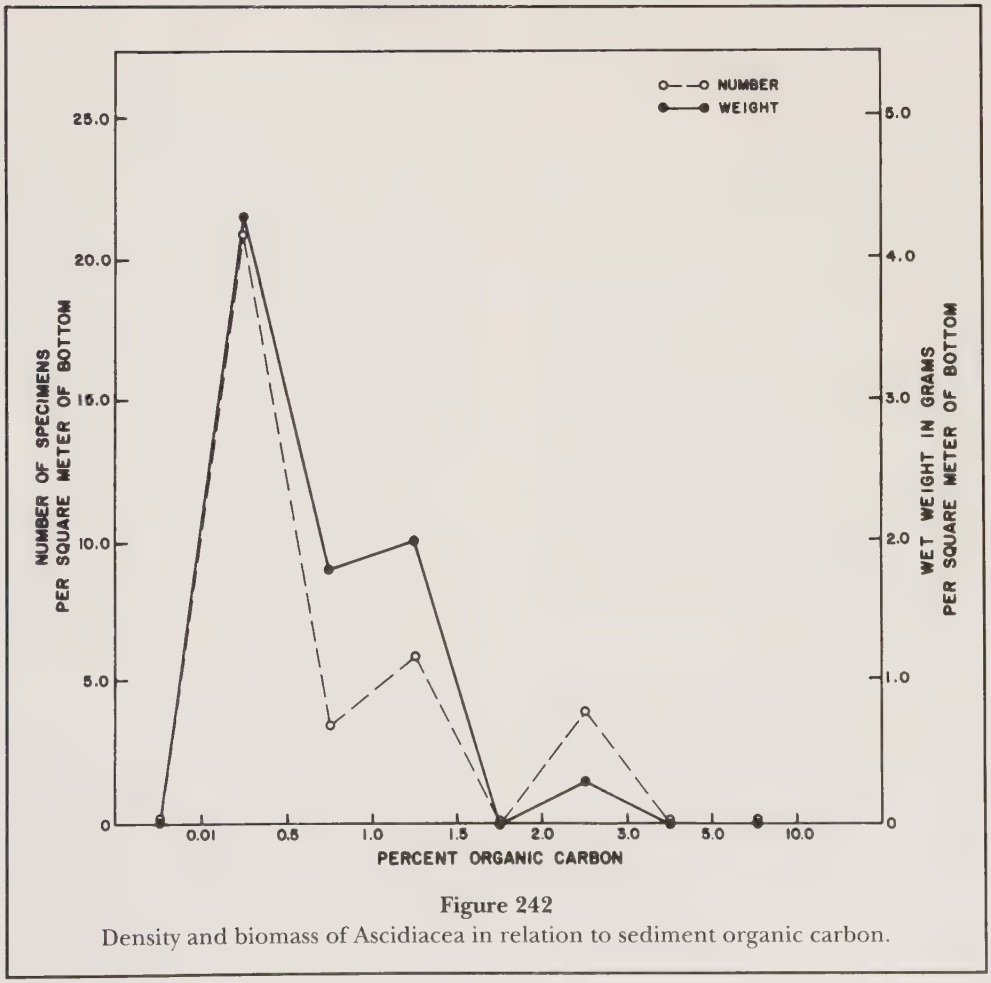


Figure 242
Density and biomass of Ascidiacea in relation to sediment organic carbon.

Frequency of Occurrence

Among the four dominant taxa, Annelida was the most ubiquitous in distribution, occurring in 96% of all stations sampled (Table 5). Next in order were members of Mollusca, which occurred in 88% of all samples, followed by Crustacea in 85% of the samples; echinoderms ranked fourth with a 72% occurrence rate.

For comparative purposes, some nondominant taxa showed intermediate frequencies; among these were Coelenterata, which occurred in 42% of the samples, and Nemertea and Sipunculida with frequencies of 34% and 23%, respectively. Ascidiacea, Bryozoa, Aschelminthes, Porifera, Brachiopoda, Pogonophora, Turbellaria, and Hemichordata were encountered with diminishing frequencies ranging from 17% to <1%.

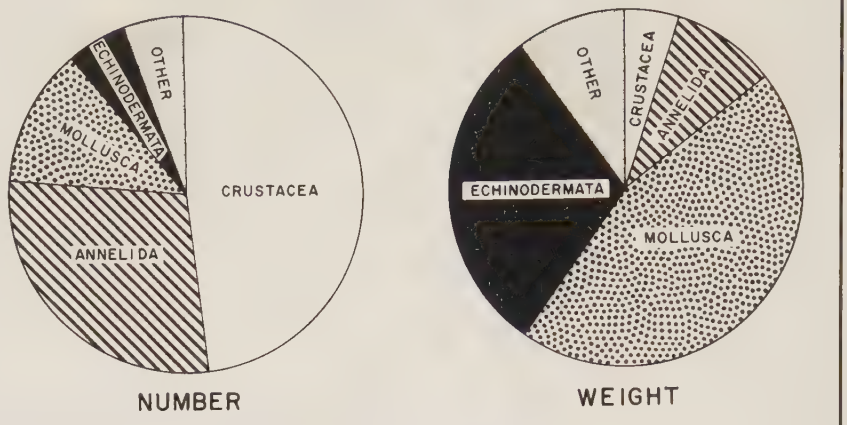


Figure 243
Percentage composition of the dominant components of the macrobenthic invertebrate fauna expressed in terms of number of individuals and wet weight of the total fauna.

Percentage Composition

The four dominant macrobenthic components collectively contributed more than 90% of the total number of individuals, and 90% of the accumulated wet weight of the macrobenthos sampled within the New England region. The relative contribution and ranking of the four, however, differed markedly between the two measures of abundance (Fig. 243).

Crustacea, with Amphipoda providing the single largest amount of individuals, was the highest ranking taxonomic component in terms of density, accounting for nearly one half (48%) of all individuals within the region. Annelida ranked second, providing slightly more than 28% of the total number of individuals encountered; Mollusca and Echinodermata followed, contributing somewhat more than 12% and 5% of the total number of individuals, respectively.

The biomass ranking was nearly the reverse of that for density. Mollusca, with Bivalvia predominating, ranked first in biomass versus third in density, contributing 46% of the total weight. Echinodermata ranked second versus fourth; Annelida ranked third versus second; and Crustacea, first in density, ranked fourth in biomass.

The differences in rank order between the two measures of abundance are attributable to size differences within the various taxonomic groups.

Geographic Distribution

The geographic distribution of density and biomass of each of the four dominant components of the macrobenthos of the New England region is depicted in Figures 69, 99, 146, and 202. Within the subareas of the region, the rank order of the four dominant taxa varied in terms of density and biomass (Figs. 13B, 14B; Tables 6, 8). In the Nova Scotia subarea, Annelida ranked first in density (648/m^2) but third in biomass (19 g/m^2); Crustacea was second in density (329/m^2) but fourth in biomass (17 g/m^2); Mollusca, third in density (77/m^2), was first in biomass (54 g/m^2); while Echinodermata fourth in density (24/m^2), was second in terms of biomass (39 g/m^2).

In the Gulf of Maine, mollusks (306/m^2) replaced annelids (29/m^2) as the dominant taxon in terms of density, the latter occupying second place, whereas mollusks were second (32 g/m^2) and annelids third (16 g/m^2), in biomass. Crustaceans (150/m^2) and echinoderms (43/m^2) ranked third and fourth, respectively, in density but were fourth (2 g/m^2) and first (56 g/m^2), respectively, in biomass.

On Georges Bank, the crustaceans (1052/m^2)were nearly twice as abundant as the annelids (546/m^2), almost nine times denser than echinoderms (121/m^2), and 22 times denser than mollusks (47/m^2). In terms of biomass, however, the echinoderms (120 g/m^2) outweighed mollusks (80 g/m^2) by 1.5 times, and crustaceans (10 g/m^2) and annelids (8 g/m^2) by 12 and 15 times, respectively.

In the Southern New England Shelf subarea, density was dominated by crustaceans (1385/m^2), followed by annelids (531/m^2), mollusks (244/m^2) and echinoderms (123/m^2) in terms of density. Mollusk biomass (171 g/m^2) was dominant in this subarea followed by significantly smaller amounts of echinoderm (36 g/m^2), annelid (30 g/m^2), and crustacean (17 g/m^2) biomass.

The two continental slope subareas contained lower densities and biomasses of all components than the shelf subareas. The mean densities and biomass on Georges Slope for the major taxa were as follows: Crustacea, 138/m^2 and 0.6 g/m^2; Mollusca, 83/m^2 and 2.7 g/m^2; Annelida, 80/m^2 and 4.9 g/m^2; and Echinodermata, 19/m^2 and 3.9 g/m^2. Southern New England Slope values were Annelida, 149/m^2 and 4.3 g/m^2; Mollusca, 58/m^2 and 1.2 g/m^2; Arthropoda, 22/m^2 and 0.1 g/m^2; Echinodermata, 19/m^2 and 10 g/m^2.

Selected Genera and Species—This section deals with the geographic distribution of 24 selected genera and species of macrobenthic invertebrates. These particular forms were selected because of their common occurrence, regional ubiquity, or distinctive distribution. Figures 244 to 249 depict the distributions of the selected forms.

Phylum Annelida

Aphrodita hastata (Moore) (Fig. 244). Commonly known as the sea mouse, this polychaete bristle worm of the family Aphroditidae may attain lengths up to 150 mm (6 inch); smaller individuals are often found in haddock, cod and red hake stomachs. It commonly inhabits mud bottoms, or mixed bottoms with a high mud content.

Scalibregma inflatum (Rathke) (Fig. 244). This medium-sized (1–5 cm) polychaete is a member of the family Scalibregmidae. An important food of many demersal fish, this species inhabits silty sand substrates.

Sternaspis scutata (Renier) (Fig. 244). This moderately small (1 cm), burrowing polychaete is stout in appearance and is a member of the family Sternaspidae; it is found in the diet of winter flounder. It commonly inhabits silty sediments.

Phylum Mollusca

Arctica islandica (Linnaeus) (Fig. 244). This rather large (18–15 cm) commercially harvested bivalve, known as the ocean quahog, mahogany quahog, or black clam, belongs to the family Arcticidae. It is a very slow-growing species that occurs very abundantly in some localities on the continental shelf. Small to medium-sized individuals are preyed upon by cod and several species of starfish. It usually inhabits muddy sand bottoms.

Astarte undata Gould (Fig. 245), the common wavy astarte of the family Astartidae, is a medium-sized (2.5–3.8 cm) bivalve. In the New England region, it is most prevalent at mid-shelf depths (50–99 m) in sand and till substrates. Although juvenile specimens are occasionally found in fish stomachs, it is not a major prey item of demersal fishes.

Cerastoderma pinnulatum (Conrad) (Fig. 245), the northern dwarf cockle, is a common, moderately small (1 cm) bivalve belonging to the family Cardiidae. This species is infrequently found in fish stomachs. It prefers sandy substrates but does occupy, in lower abundance, other types of sediments.

Cyclocardia borealis (Conrad) (Fig. 245), the northern cyclocardia, is a medium-sized (3–5 cm) bivalve of the family Carditidae. Broadly distributed throughout the region, it prefers sand and till substrates but does occur in other sediments as well. It is not common in fish diets.

Modiolus modiolus (Linnaeus) (Fig. 245), the northern horse mussel, is the largest (5–15 cm) and most common mussel of the offshore New England region; it is a member of the family Mytilidae. It is found on the periphery of the Gulf of Maine and on Georges Bank, and extends onto the Southern New England Shelf. It prefers sand and sand-shell substrates.

Placopecten magellanicus (Gmelin) (Fig. 246), the sea scallop, is one of the most valuable commercial shellfish resources of the U.S. East Coast, especially in the New England region. It is a large bivalve (12–20 cm) of the family Pectinidae, found most abundantly on coarse sandy bottoms. In addition to harvest by man, juveniles of this species are found in the diets of some demersal fishes, principally haddock, and ocean pout.

Buccinum spp. (Fig. 246) is represented in our samples by four species in the family Buccinidae. The species represented are *B. elatius, B. gouldi, B. hydrophanum,* and *B. undatum.* Among the four species, the moderately large (5–10 cm) *B. undatum,* the waved whelk, is overwhelmingly the most common form. They are typically found at mid- to lower-shelf depths in sand and coarser grained sediments.

Neptunea decemcostata (Say) (Fig. 246), the wrinkled whelk, is a moderately large (7–11 cm) gastropod belonging to the family Buccinidae. This species typically inhabits hard bottoms ranging from coarse sand to gravels at mid- to lower-shelf depths.

Phylum Arthropoda

Ampelisca agassizi (Judd) (Fig. 246), this gammaridean amphipod of the family Ampeliscidae is a medium-sized (4–7 mm) tube dweller. It is the most abundant and common species of amphipod in the southwestern half of the study area; in some localities it is exceptionally abundant. It prefers a sandy substratum. This species is a very common prey in the diet of many demersal fish.

Leptocheirus pinguis (Stimpson) (Fig. 247), a species of gammaridean amphipod, family Aoridae, is a moder-

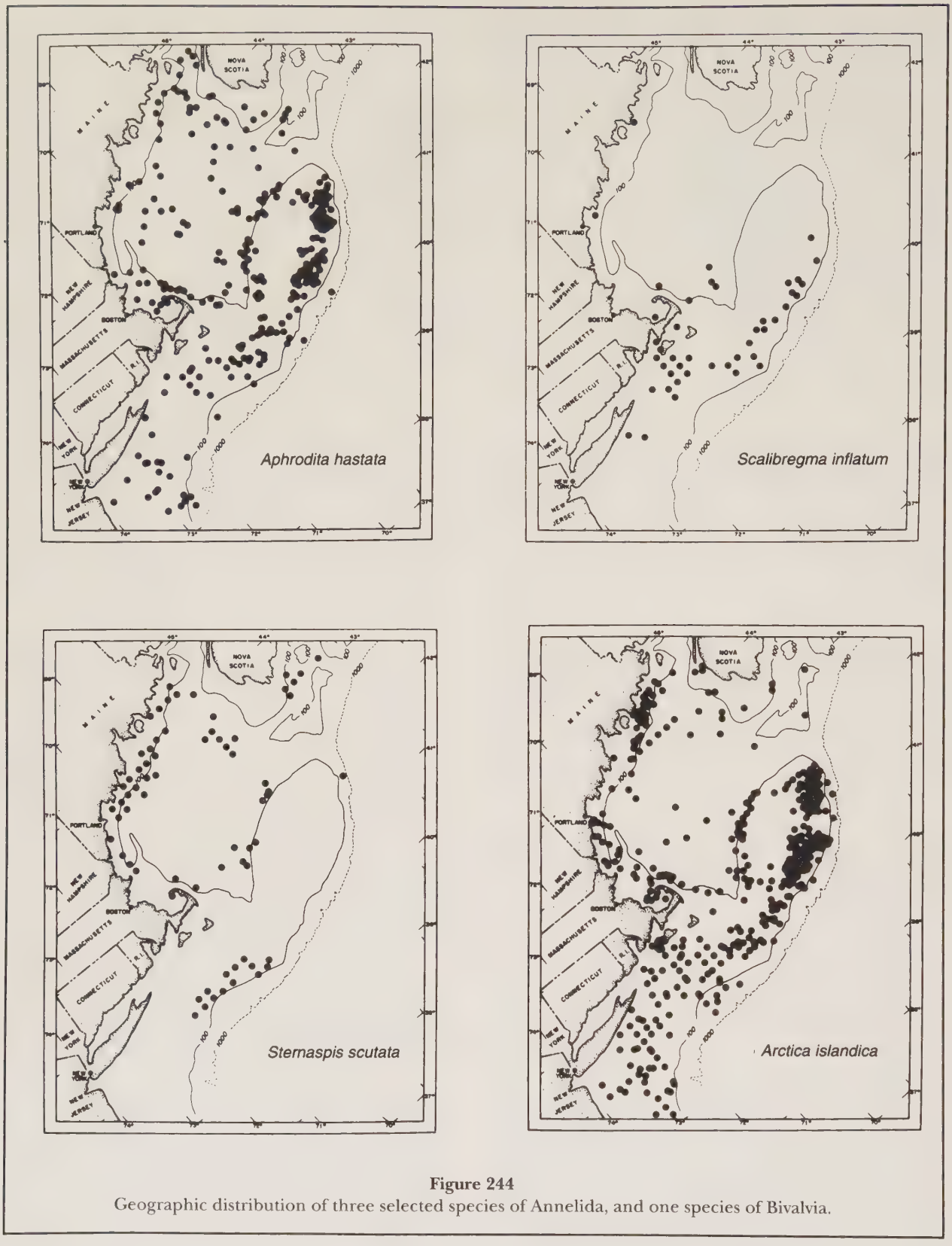
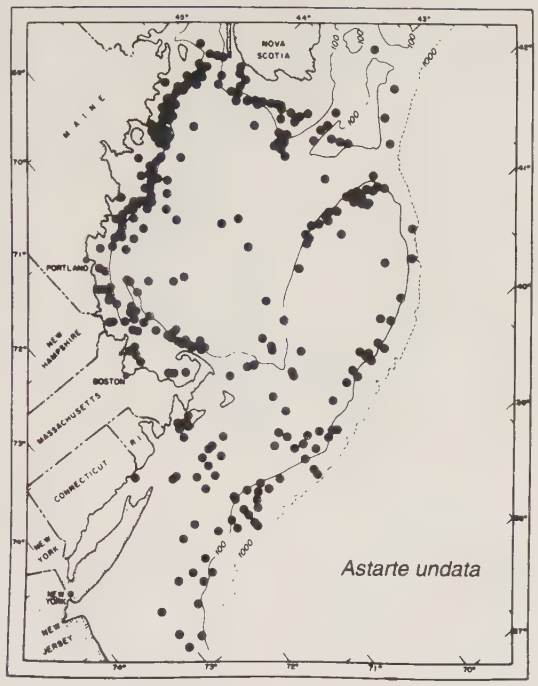
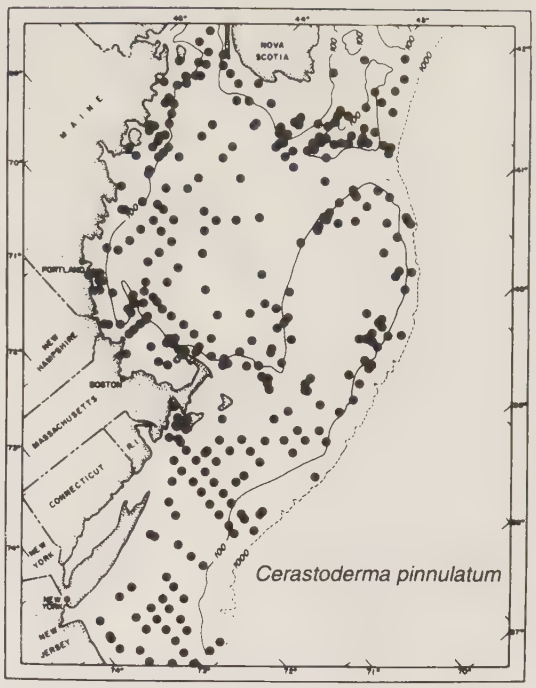
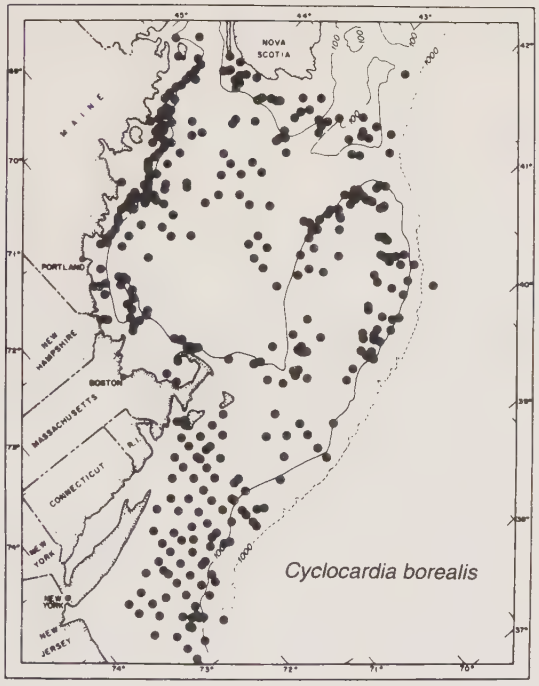


Figure 244
Geographic distribution of three selected species of Annelida, and one species of Bivalvia.







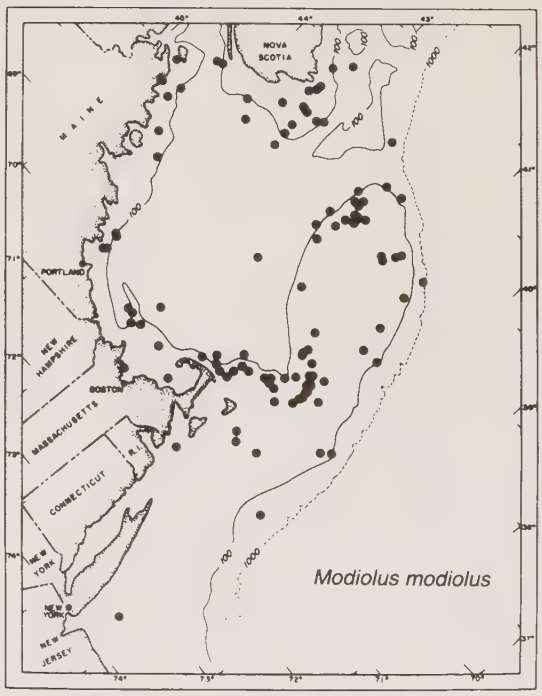


Figure 245
Geographic distribution of four selected species of Bivalvia.

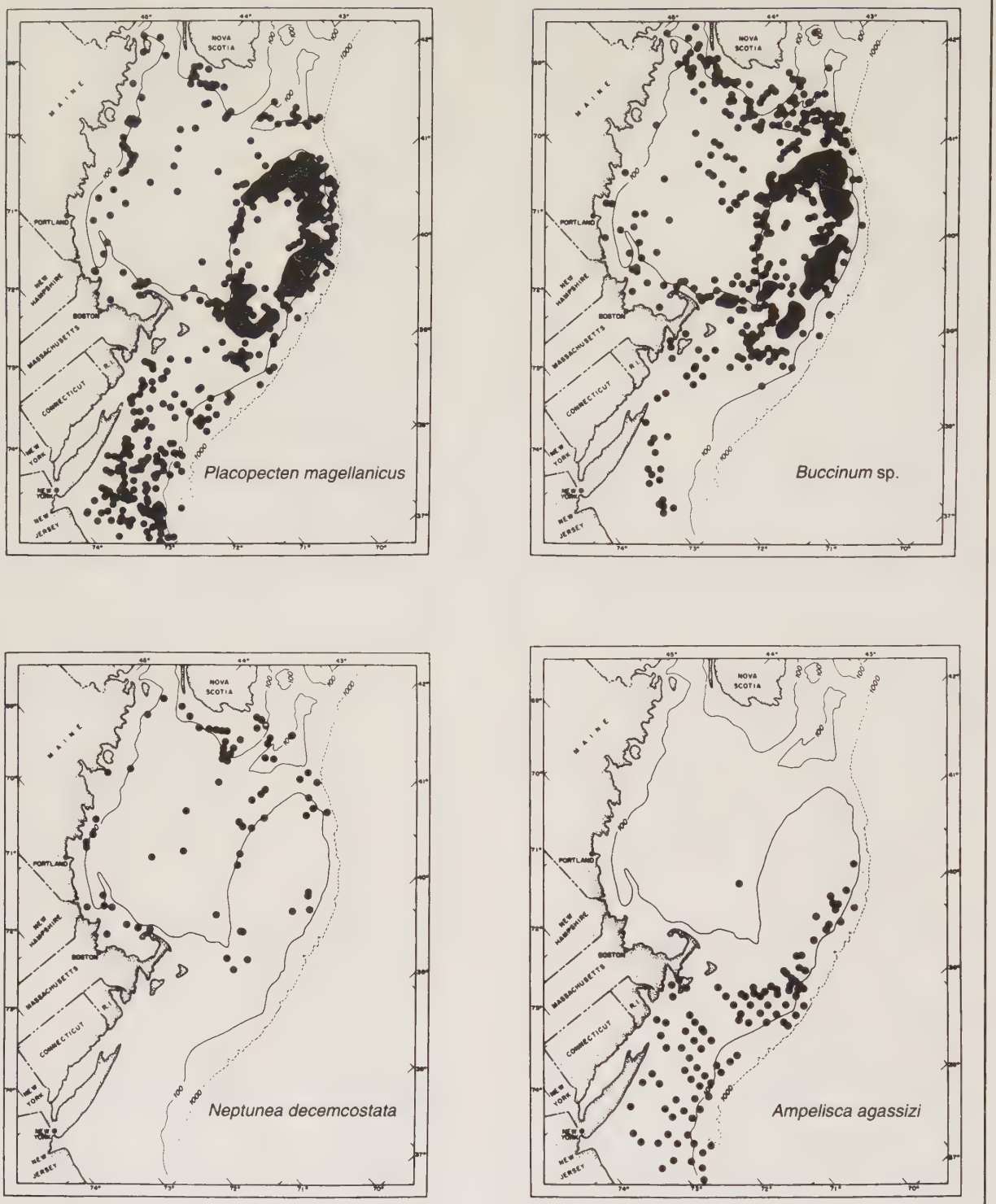
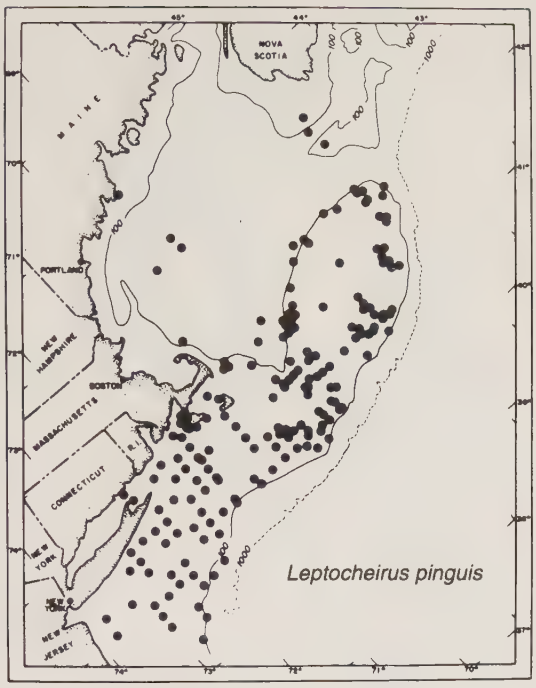
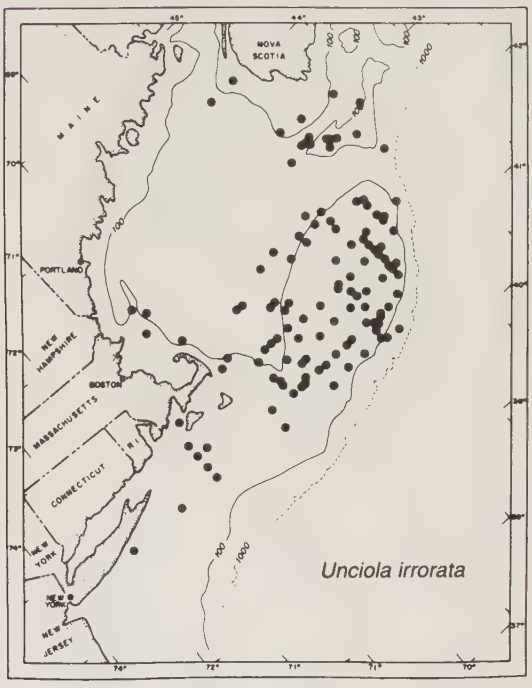
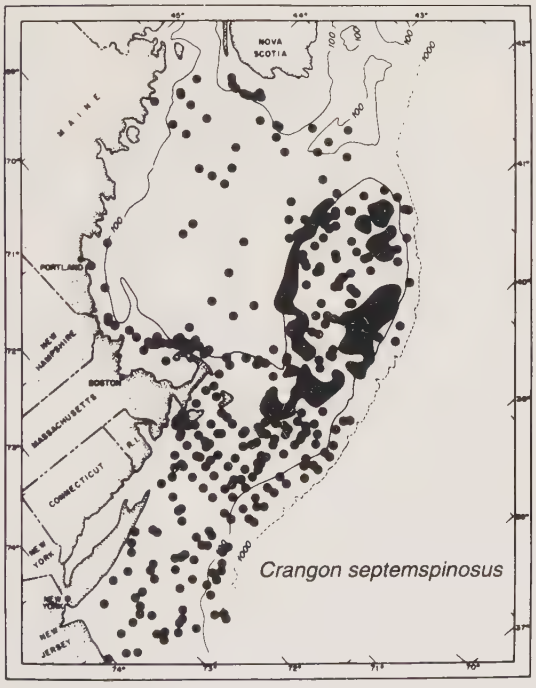


Figure 246

Geographic distribution of one selected species of Bivalvia, one genus and one species of Gastropoda, and one species of Amphipoda.







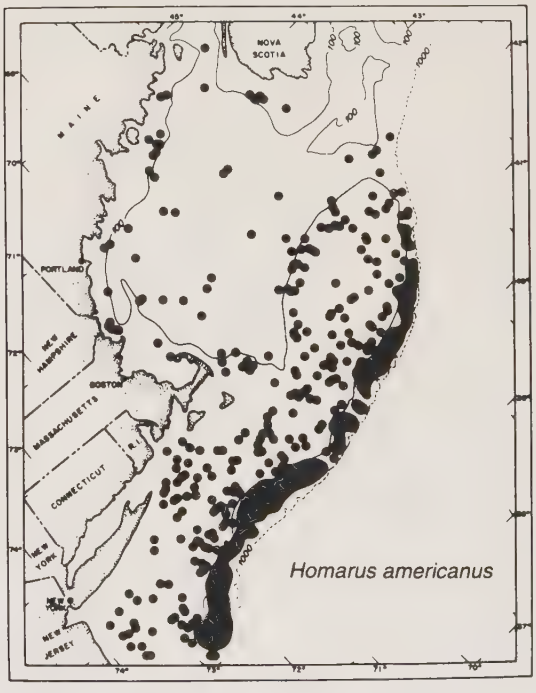


Figure 247
Geographic distribution of two selected species of Amphipoda, and two of Decapoda.

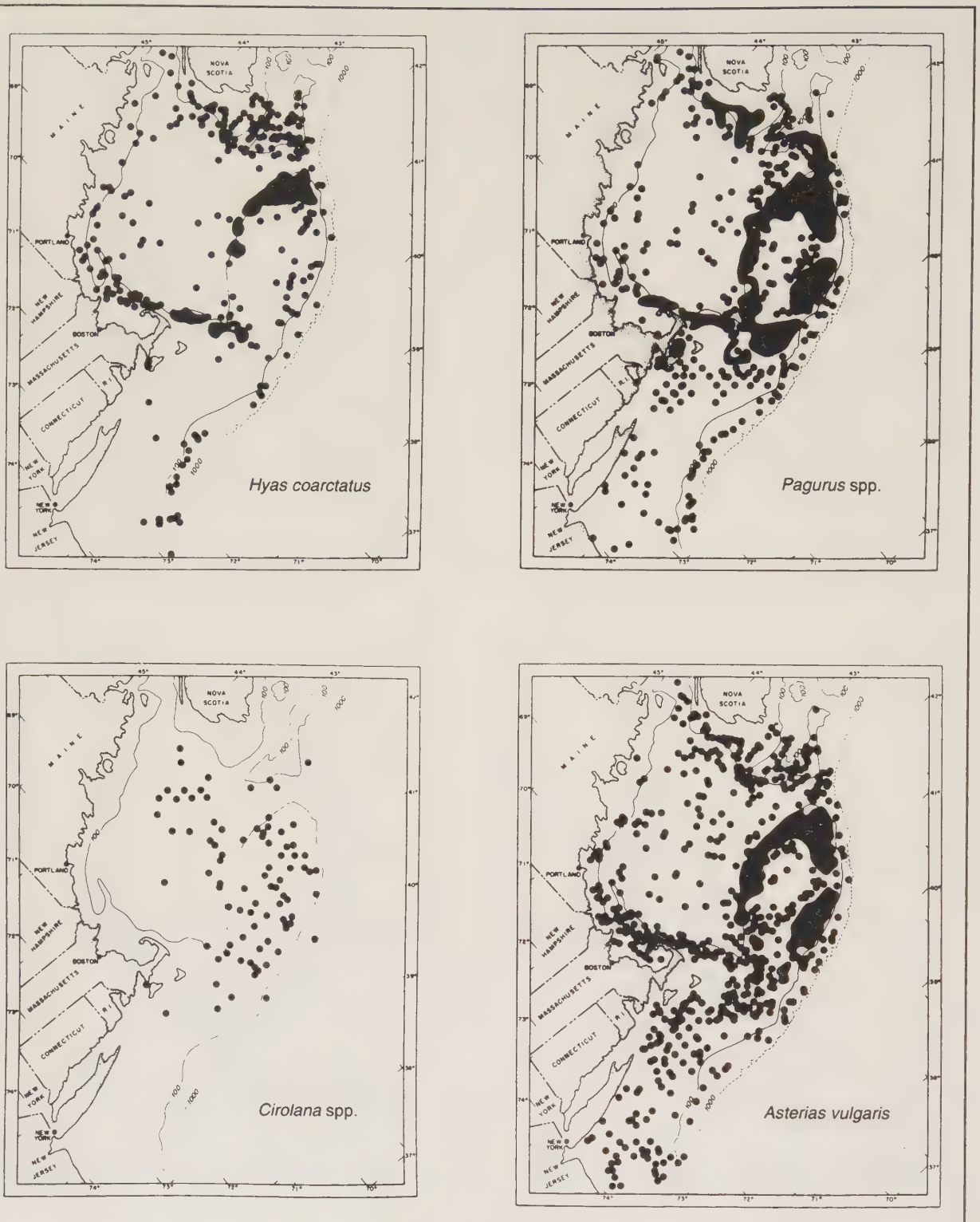
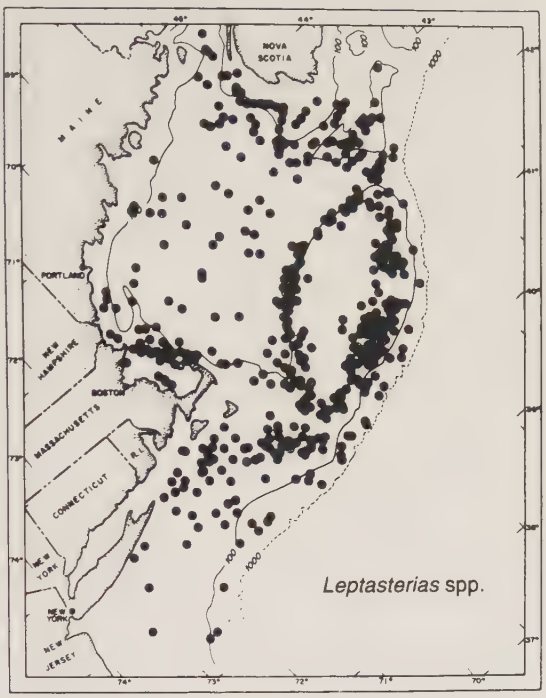
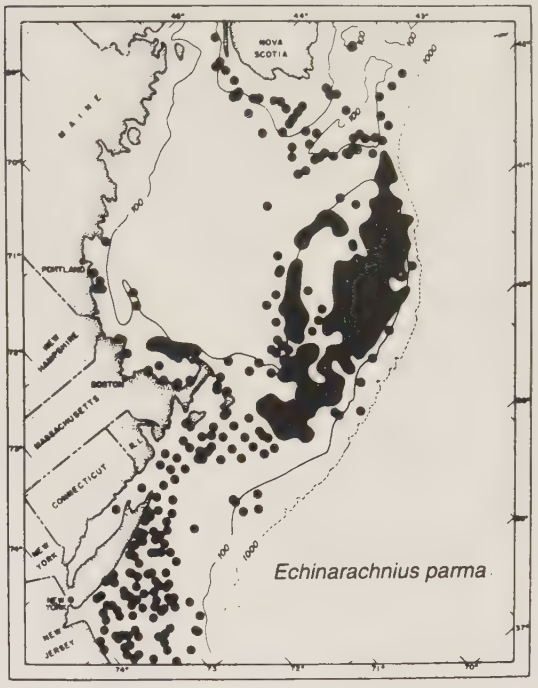
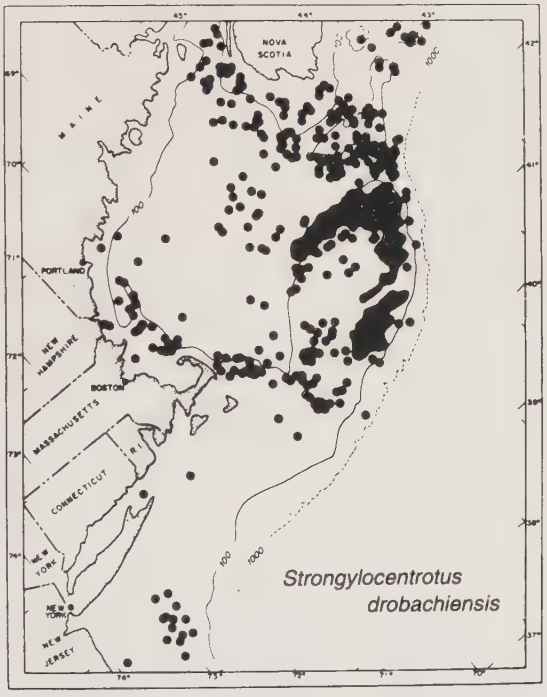


Figure 248

Geographic distribution of one species and one genus of Decapoda, one genus of Isopoda, and one species of Asteroidea.







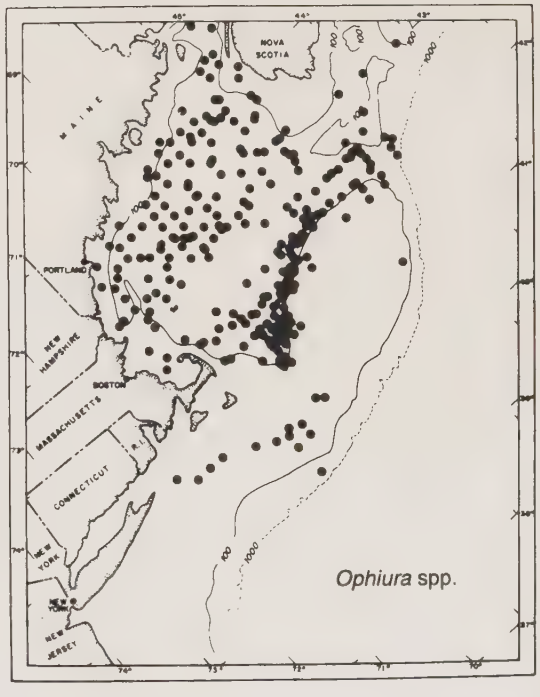


Figure 249
Geographic distribution of one genus of Asteroidea, two species of Echinoidea, and one genus of Ophiuroidea.

ately large (10–17 mm) and abundant tube-dwelling inhabitant of continental shelf sandy substrates. It is very important in demersal fish diets.

Unciola irrorata (Say) (Fig. 247), another moderate-sized (10–13 mm) tube-dwelling gammaridean amphipod of the family Aoridae, is abundant in the sands of Georges Bank and is also very important in demersal fish diets.

Crangon septemspinosa Say (Fig. 247), the sevenspined bay shrimp, a moderately small (5–8 cm) caridean shrimp of the family Crangonidae. It is typically found in sandy sediments of the region in both inshore and continental shelf waters, and in certain localities is very abundant. This shrimp is a very important prey to nearly all demersal fishes.

Homarus americanus H. Milne-Edwards (Fig. 247), the American lobster, is, together with the sea scallop, one of the most commercially valuable invertebrate resources of the northwest Atlantic. It is widely distributed throughout the New England region from inshore bays and sounds to the offshore canyons bisecting the edge of the continental shelf. Size of mature lobsters ranges from around 25 cm average length, for individuals captured for market by the inshore fishery, to very large (sometimes in excess of 80 cm), for specimens in the offshore stock; minimum legal size for capture is currently 8.13 cm (3.25 inch). Lobsters are scavengers and inhabit a variety of substrates.

Hyas coarctatus Leach (Fig. 248), the arctic lyre crab, is a moderately small (to 31 mm) spider crab in the family Majidae. This species is common throughout the New England region on muddy and pebbly bottoms. Small individuals have been reported to occur occasionally in the diet of long-horned sculpin.

Pagurus spp. (Fig. 248) comprise seven species of pagurid hermit crabs resident in the New England region. The species of the genus *Pagurus* in the family Paguridae represented in this study include *P. acadianus, P. annulipes, P. arcuatus, P. longicarpus, P. politus, P. pollicaris,* and *P. pubescens.* The represented species range from small to medium in size (9–31 mm, carapace length), are ubiquitous throughout the region in nearly all substrate types, and are preyed upon by bottom fishes. The most common and broadly distributed species is *P. acadianus.*

Cirolana spp. (Fig. 248), comprise three species of the isopod crustacean family Cirolanidae resident in the study area (*C. concharum, C. impressa,* and *C. polita*) along with several others identified only to the generic level. These moderately small (16–23 mm) crustaceans are fairly common on muddy and sandy bottoms in the Gulf of Maine and on Georges Bank. They are prey to a variety of demersal fishes.

Phylum Echinodermata

Asterias vulgaris Verril (Fig. 248), the northern starfish or purple star, is one of the most common starfishes inhabiting the offshore waters of the New England region and is a member of the family Asteriidae. This is a large species commonly between 15 cm and 30 cm (6–12 inch) in diameter; some specimens up to 42.5 cm (17 inch) have been reported from the northern limits of its range. It is normally found on sandy bottoms where it is a very important predator of bivalve mollusks. Juvenile specimens are occasionally encountered in fish stomachs.

Leptasterias spp. (Fig. 249), which represent several species of the genus *Leptasterias,* also of the family Asteriidae, are common inhabitants of the New England Region on sandy bottoms. These brightly, but variably, colored species are of moderate size (5–10 cm) and in some localities are very abundant. Small specimens are occasionally preyed upon by some species of groundfish.

Echinarachnius parma (Lamarck) (Fig. 249), the northern sand dollar, is the most abundant urchin (class Echinoidea, family Scutellidae) of the New England region; it is so abundant in some localities of Georges Bank that the bottom resembles a mosaic pavement. As its common name implies, it is a sand dweller. Sand dollars of the region are typically 7.5 cm in diameter. They are a common prey of flounders, haddock and cod.

Strongylocentrotus droebachiensis (Müller) (Fig. 249), another ubiquitous echinoid (family Strongylocentrotidea), the green sea urchin, is a hard bottom dweller for whose popular roe a commercial fishery, inactive since the 1930's and 1940's, is reemerging in northeastern U.S. and Canadian waters. Size ranges from 5 cm to nearly 9 cm. Haddock and American plaice prey on this spiny morsel.

Ophiura spp. (Fig. 249) comprise three species and some undetermined specimens of this genus of brittle stars (family Ophiolepididae) inhabiting the New England region; included are *O. ljungmani, O. robusta, O. sarsi,* and unidentified species. Members of this group are widely distributed and occur in most sediment types. Size of the central disc ranges from 10 to 38 mm. They are common in the diets of haddock and American plaice.

Bathymetric Distribution

In the New England region density and biomass of the major taxa generally decreased with increasing water depth (Tables 11, 13; Figs. 15, 16). Crustacea was the dominant component of the fauna, in terms of density, in shallow and continental shelf depths, ranging from 1,351 to 169 individuals/m^2. Substantially lower densities occurred in waters deeper than 200 m. Annelida had the next highest densities in shallow waters (719/m^2) and at continental shelf depths (519–437/m^2). Moderate numbers (241–107/m^2) occurred at conti-

nental slope depths, and low densities (9–30/m^2) were encountered at lower slope and upper rise depths. Mollusca showed a similar pattern of density distribution with depth; density was greatest (570/m^2) in shallow water, moderate (136–205/m^2) at shelf depths, and moderately low in deeper waters. However, mollusks were numerically dominant at the deeper depths. Echinoderm density was greatest (133/m^2) at mid-shelf depths between 25 m and 49 m, moderate (87–95/m^2) in deeper shelf water, and decreased with increasing depth beyond 200 m. Moderately low densities (47/m^2) occurred in shallow (0–24 m) water.

Mollusca was the dominant faunal component of biomass at nearly all depths. Greatest biomass (258 g/m^2) occurred in shallow water (0–24 m) with values moderately high (132–21 g/m^2) at shelf depths and diminishing rapidly at depths below 200 m. Echinoderm biomass was greatest (167–106 g/m^2) in waters of 49 m and less, decreased to 34 g/m^2 at outer shelf depths, but dominated at depths beyond 200 m (1.7–19 g/m^2). Annelida biomass was highest (27 g/m^2) in shallow (0–24 m) water and nearly equal (25 g/m^2) in water depths between 50 m and 99 m. Values ranged between 15 g/m^2 and 16 g/m^2 at other continental shelf depths but decreased rapidly with increasing depth beyond 200 m. Crustacea, although numerically dominant, ranked fourth in biomass at nearly all depths except the shallowest one (0–24 m) where a value of 37 g/m^2 placed them third. Biomass of crustaceans ranged from 2 to 16 g/m^2 at continental shelf depths (25–199 m), with a rapid decrease from 4 g/m^2 at 200–499 m to approximately 0.1 g/m^2 in slope and rise waters.

Relation to Bottom Sediments

Numerical abundance of the four dominant faunal components in relation to the six major sediment types encountered in the New England region did not exhibit any trend as dramatic as that for depth (Tables 16, 18; Fig. 17). Annelids seemed to prefer sand (558/m^2), gravel (505/m^2), and shell (443/m^2) bottoms but were moderately abundant in till, sand-silt, and silt-clay bottoms as well. Mollusks were generally more abundant in silt-clay (354/m^2), shell (229/m^2), and sand-silt (276/m^2) but were found in somewhat lower abundance in other sediments also. Crustacea were most abundant in sand (1,336/m^2), gravel (710/m^2), and sand-silt (275/m^2) and were found in diminishing amounts in shell (124/m^2), till (59/m^2), and silt-clay (34/m^2). Sand-silt (104/m^2) and sand (95/m^2) contained the most echinoderms, followed by till and silt-clay (67/m^2 and 65/m^2, respectively), then shell (28/m^2) and gravel (23/m^2).

Density rank order in the various sediments listed by decreasing particle size was as follows: gravel: Crustacea, Annelida, Mollusca, Echinodermata; till: Annelida, Mollusca, Echinodermata, Crustacea; shell: Annelida, Mollusca, Crustacea, Echinodermata; sand: Crustacea, Annelida, Mollusca, Echinodermata; sand-silt: Annelida, Mollusca and Crustacea equal, Echinodermata; silt-clay: Mollusca, Annelida, Echinodermata, Crustacea.

The distribution of the biomass of the major taxa among the various sediment types was fairly even. The annelids showed the greatest uniformity with the smallest biomass (11 g/m^2) in till and largest (26 g/m^2) in sand-silt. Biomass ranged from 15 to 16 g/m^2 in the four other types. Mollusks showed some variability, with shell bottoms containing the largest biomass (168 g/m^2) and till the smallest (6 g/m^2). Molluscan biomass in gravel was 94 g/m^2, in sand 121 g/m^2, in sand-silt 74 g/m^2, and in silt-clay 18 g/m^2. Crustacean biomass was 20 g/m^2 in gravel and 12 g/m^2 in sand; 7 g/m^2 and 6 g/m^2 in sand-silt and shell, respectively, and 2 g/m^2 and 0.6 g/m^2 in till and silt-clay ,respectively. Echinoderm biomass was greatest in sand (88 g/m^2), 43 g/m^2 in silt-clay, and 37 g/m^2 in sand-silt. Median amounts occurred in till (15 g/m^2) and lower amounts in gravel (6 g/m^2) and shell (3 g/m^2). Biomass rank order in bottom sediments was as follows: gravel: Mollusca, Crustacea, Annelida, Echinodermata; till: Echinodermata, Annelida, Mollusca, Crustacea; shell: Mollusca, Annelida, Crustacea, Echinodermata; sand: Mollusca, Echinodermata, Annelida, Crustacea; sand-silt: Mollusca, Echinodermata, Annelida, Crustacea; and silt-clay: Echinodermata, Mollusca, Annelida, Crustacea.

Relation to Water Temperature

Among the four dominant taxa there were no clear-cut trends discernible with regard to the annual range in bottom water temperature (Tables 21, 23; Fig. 18). Where ranges of temperatures were between 8 and 19.9°C, Crustacea was the numerically dominant taxon, with densities ranging from 768 to 1,475 individuals per m^2, whereas annelids dominated in areas exhibiting rather stable annual temperature regimes, between 0 and 7.9°C (212–513 individuals per m^2), and in areas experiencing the broadest temperature range of 20–23.9°C, where mean densities of 1,698 individuals per m^2 were found. Densities of Mollusca and Echinodermata were fairly consistent at moderate levels (84–345/m^2 for Mollusca and 21–171/m^2 for Echinodermata) throughout the temperature range spectrum. Mollusca, however, did make a strong showing (1,242 individuals/m^2) where the range in annual temperature was broadest.

Rank order of dominance for the major taxa in the six annual temperature range classes in terms of density was as follows: 0–3.9°C: Annelida, Crustacea, Echi-

nodermata, Mollusca; 4–7.9°C: Annelida, Crustacea, Mollusca, Echinodermata; 8–11.9°C: Crustacea, Annelida, Mollusca, Echinodermata; 12–15.9°C: Crustacea, Mollusca, Annelida, Echinodermata; 16–19.9°C: Crustacea, Annelida, Mollusca, Echinodermata; 20–23.9°C: Annelida, Mollusca, Crustacea, Echinodermata.

The relationship of the dominant taxa biomasses to annual range of bottom water temperature was similar to that of density in that no definite trends were evident. However, a marked change in dominance ranking prevailed, wherein the density dominants (crustaceans and annelids) were replaced by echinoderms and mollusks as the leading contributors to biomass in nearly all temperature range regimes. Echinodermata dominated biomass in four of the six temperature range classes, including the narrowest and broadest ranges; their mean biomass ranged from 12 to 263 g/m^2. Mollusk biomass, second to that of echinoderms in most temperature ranges, was clearly dominant where temperature ranges of 8–11.9°C and 16–19.9°C prevailed; their mean biomass was 129 g/m^2 in the former and 340 g/m^2 in the latter. The contributions of the other two dominant taxa, annelids and especially crustaceans, due to their small size, were clearly subordinate in all temperature regimes. Annelid biomass ranged from 10 to 40 g/m^2, and crustacean biomass from 1 to 25 g/m^2.

Rank order of dominance for the major taxa in the six annual temperature range classes in terms of biomass was as follows: 0–3.9°C: Echinodermata, Annelida, Mollusca, Crustacea; 4–7.9°C: Echinodermata, Mollusca, Annelida, Crustacea; 8–11.9°C: Mollusca, Echinodermata, Annelida, Crustacea; 12–15.9°C: Echinodermata, Mollusca, Annelida, Crustacea; 16–19.9°C: Mollusca, Echinodermata, Annelida, Crustacea; 20–23.9°C: Echinodermata, Mollusca, Annelida, Crustacea.

Relation to Sediment Organic Carbon

As mentioned above (see section "Total Macrobenthos") there was no clear-cut correlation between sediment organic carbon content and faunal abundance except in a few exceptional cases (Tables 26, 28; Fig. 26).

The numerical abundance of the dominant taxa varied widely in relation to organic carbon content for all except Echinodermata. This taxon ranked fourth in all organic carbon content classes except two (0.00% and 1.00–1.49%) where it ranked third, slightly ahead of Crustacea. Density of echinoderms was moderately low, ranging from only 3–91 individuals per m^2. Crustacean density varied widely among the various carbon content classes, ranging from 21 to 1,357/m^2. Greatest abundances occurred in carbon content levels of 0.01–0.49% (1,066/m^2) and 3.00–4.99% (1,357/m^2), with moderately low to fairly high densities occurring in carbon content levels between these two. Lowest densities (21–22/m^2) prevailed in areas where no measurable carbon existed as well as in areas where the greatest amounts of carbon were measured. Mollusca, was one exception, showing a positive correlation of generally increasing density with increasing carbon, ranging from 69/m^2 in areas devoid of carbon to 1,120/m^2 where carbon was between 3.0% and 4.9%. No mollusks occurred where carbon content exceeded 5%. Annelida were present in all organic carbon content classes. Their density was significantly lower at both extremes of the carbon content spectrum (between 11/m^2 and 81/m^2) compared with their abundance (196–504/m^2) in areas containing low (0.01–0.49%) to moderate (2.0–2.99%) amounts of carbon.

Rank order of the numerical abundance of the dominant taxa with regard to organic carbon content was as follows: 0%: Mollusca, Annelida, Echinodermata, Crustacea; 0.01–0.49%: Crustacea, Annelida, Mollusca, Echinodermata; 0.50–0.99%: Annelida, Crustacea, Mollusca; Echinodermata; 1.00–1.49%: Mollusca, Annelida, Echinodermata, Crustacea; 1.50–1.99%: Mollusca, Annelida, Crustacea, Echinodermata; 2.00–2.99%: Crustacea, Mollusca, Annelida, Echinodermata; 3.00–4.99%: Crustacea, Mollusca, Annelida, Echinodermata; 5.00%+: Crustacea, Annelida; no Mollusca or Echinodermata were found in this class.

Similar to numerical abundance, biomasses of dominant taxa showed no clear-cut correlation to the organic carbon content of the bottom sediments. Most notable was the considerable echinoderm biomass in all but the highest carbon content classes, compared with its low numerical density. Highest mean biomasses (105 g/m^2 and 562 g/m^2) occurred in areas with moderately high carbon contents (between 2% and 4.99%), and lowest (6 g/m^2) occurred in areas devoid of measurable organic carbon. Moderate biomasses, ranging from 23 to 44 g/m^2, occurred in areas with low to intermediate carbon content levels (0.01–1.99%). Mollusca, also absent where the highest measures of organic carbon occurred, nevertheless showed a preference for some organic carbon content, with highest biomasses (812 g/m^2 and 227 g/m^2) occurring in the two carbon content classes between 2.0 and 4.99%. However, moderately high biomass (132 g/m^2) was also found where carbon levels were only between 0.01 and 0.49%. Lowest biomass (only 0.8 g/m^2) occurred in sediments devoid of carbon. Moderate levels of biomass (25–13 g/m^2) occurred in organic carbon levels that ranged from 0.50 to 1.99%. The mean biomass of Annelida was fairly consistent at moderate levels ranging between 11 g/m^2 and 27 g/m^2 in areas of organic carbon content ranging between 0.01 and 4.99%. Lowest mean biomass of annelids (0.11 g/m^2) occurred in the highest carbon content class (5+%) and intermediate amounts (7 g/m^2) were found where measurable

carbon was absent in the sediments. Crustacean mean biomass ranged from a low of 0.11 g/m^2 in areas of highest organic carbon content to a high of 19 g/m^2 where organic carbon was between 2% and 2.99%. Moderately low biomasses (between 1 g/m^2 and 9 g/m^2) occurred in the other carbon content classes. Areas devoid of organic content also contained low mean biomass (0.31 g/m^2).

Rank order of the mean biomass of the dominant taxa in terms of organic carbon content was as follows: 0%: Annelida, Echinodermata, Mollusca, Crustacea; 0.01–0.49%: Mollusca, Echinodermata, Annelida, Crustacea; 0.50–0.99%: Mollusca, Echinodermata, Annelida, Crustacea; 1.00–1.49%: Echinodermata, Mollusca, Annelida, Crustacea; 1.50–1.99%: Echinodermata, Annelida, Mollusca, Crustacea; 2.00–2.99%: Mollusca, Echinodermata, Annelida, Crustacea; 3.00–4.99%: Echinodermata, Mollusca, Annelida, Crustacea; 5.00%+: Annelida and Crustacea were equal, whereas Mollusca and Echinodermata were absent in this class.

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